Deadwood in Forest Ecosystems

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1. Introduction

Until recently, deadwood was perceived as a negative element of forest ecosystems, that indicates "mismanagement, negligence, and wastefulness" of the applied forest management (Stachura et al., 2007). It was regarded as a potential source of biotic pests, mainly insects (Bütler, 2003; Marage & Lemperiere, 2005), to remaining trees in a forest as well as to adjacent stands (Pasierbek et al., 2007). The presence of deadwood was also seen as a threat of the spread of abiotic disturbances, e.g fire (Thomas, 2002; Travaglini et al., 2007). In managed stands, deadwood represented an obstacle to silvicultural activities (Travaglini & Chirici, 2006; Travaglini et al., 2007), and reforestation (Thomas, 2002). Considering forest workers and visitors, standing dead trees have been seen as a threat to public safety (Peterken, 1996; Thomas, 2002) that had to be removed immediately after they had occurred (Pasierbek et al., 2007). For these reasons, sanitary cuttings have been common forestry activities not only in managed forests, but also in protected areas (Pasierbek et al., 2007; Stachura et al., 2007). In Europe, the maintenance of "hygienic standards" of a forest through systematic removal of sick, dying, and dead trees has been a common practice for more than 200 years (Stachura et al., 2007). In traditional systems, nearly every piece of wood would have been utilised (Mössmer, 1999; Butler et al., 2002). While large deadwood was usually extracted from the forests during stand tending (Radu, 2007), small wood pieces and leftovers were often burnt (Travaglini & Chirici, 2006). This intense forest exploitation has led to a substantial decrease of deadwood quantities (Travaglini & Chirici, 2006).

Over the last decades, the perception of deadwood in forest ecosystems has gradually changed as the scientific research gained information about the functions of deadwood in forests. North American researchers were the first to recognise the importance of deadwood presence in forest ecosystems (Radu, 2007). Already in the first half of the twentieth century several authors (e.g. Graham, 1925; Kimmey & Furniss, 1943; Savely, 1939, as cited in Thomas, 2002) identified deadwood as an important habitat for wildlife. In 1966 Elton (1966) described the role of deadwood in forests as a critical habitat component for a great

number of species. In America, researchers as well as forest managers recognised the importance of deadwood in the ecology of a forest as early as in the 1970s (Thomas, 2002). This triggered additional research to further expand knowledge about the role of deadwood in forest ecosystems. Since then, a number of publications have documented its importance particularly for biodiversity (Ferris & Humphrey, 1999; Humphrey et al., 2004; Müller & Schnell, 2003; Schuck et al., 2004), nutrient cycling (Harmon et al., 1986; Krankina et al., 1999; Lexer et al., 2000; Pasinelli & Suter, 2000), natural regeneration (Harmon & Franklin, 1989; Mai, 1999; Ulbrichová et al., 2006; Vorčák et al., 2005, 2006; Zielonka, 2006) and other processes.

Nowadays, deadwood is of interests not only to ecologists, but also to mycologists, foresters, and fuel specialists (Rondeux & Sanchez, 2009). It is increasingly recognised as an important component in the functioning of forest ecosystems (Vandekerkhove et al., 2009) and is becoming an integrated part of forest management (Marage & Lemperiere, 2005). This is proved by the fact that deadwood has been selected as a Pan-European indicator of sustainable forest management (Ministerial Conference of Protection of Forest Ecosystems [MCPFE], 2002). Deadwood is also one of 15 main indicators of biodiversity proposed by European Environmental Agency (Humphrey et al., 2004). Within the Forest Inventory and Analysis program in the USA, deadwood is an indicator of forest structural diversity, carbon sources and fuel loadings (Woodall & Williams, 2005).

Hence, the objectives of the presented paper are (i) to review the approaches for deadwood description, characterisation, and evaluation, (ii) to review the importance of deadwood for sustainable forest management.

Fig. 1. Deadwood as a part of natural forest ecosystem. (photo by J. Vorčák)

2. Definition and types of deadwood

Schuck et al. (2004) and Rondeux & Sanchez (2009) presented several definitions of deadwood that were gathered within the activities of COST Action E272, and thus showed the variability in understanding of this term, which mainly depends on the aim of the particular study (Rondeux & Sanchez, 2009). However, from a general perspective the term deadwood encompasses all woody material in forests that is no longer living including stems, or their parts, branches, twigs, and roots, but excluding deadwood parts of living trees. Hence, it includes both aboveground and belowground woody material (Harmon & Sexton, 1996). It can originate either from the natural mortality caused by senescence, competition, or disturbances (windthrow), or from silvicultural treatments (Rondeux & Sanchez, 2009).

The aboveground woody debris can occur as standing dead trees or shrubs or their partial remains, or as material lying on the forest floor (Pyle & Brown, 1999). Belowground material include dead woody roots and buried wood, which is very decayed woody detritus found in the mineral soil or forest floor (Harmon & Sexton, 1996). However, since belowground material is difficult to quantify (Schuck et al., 2004), it is only rarely accounted for in the studies; although its proportion may be particularly in managed forest stands significant (Debeljak, 2006).

As vary the definitions of deadwood between the studies, so do the types specified in individual works. While some authors (e.g. Atici et al., 2008; Fridman & Walheim, 2000; Christensen et al., 2005; Vacik et al., 2009) distinguish only two types of deadwood, namely standing and lying deadwood, other works use a more detailed classification with four or five deadwood components (Kirby et al., 1998; Schuck et al., 2004; Travaglini et al., 2007). The basic classifications distinguish between standing and downed or fallen deadwood, while the common separation limit is at a 45-degree angle (Harmon & Sexton, 1996; Rondeux & Sanchez, 2009). There is a clear difference in the decomposition process between the two types of deadwood and in the host species. While birds and lichens are almost entirely associated to standing dead trees, fungi and moss species primarily colonise lying deadwood (Stokland et al., 2004).

Standing deadwood consists of standing dead trees, snags, and stumps. Snags are defined as vertical pieces of dead trees. There exists a discrepancy in the understanding of snags and stumps between some authors. For example, Harmon & Sexton (1996) consider a snag any vertical piece irrespective of its height resulting from natural processes only, while Travaglini et al. (2007) require a snag to have a height equal to or greater than 1.3 m. Consequently, in the first work, a stump is defined as a short vertical piece resulting from cutting (Harmon & Sexton, 1996), but in the second paper, it is a piece shorter than 1.3 m irrespective of its origin. Lying deadwood includes downed dead trees, and lying deadwood pieces, which are often called logs. The specification of log parameters depends on a particular study. For example, Pyle & Brown (1999) define a log as a piece at least 1.5 m in length, while Debeljak (2006) considers a log any lying woody piece with length 1 m or more.

The most important size distinction is between coarse and fine woody debris (Harmon & Sexton, 1996) representing large and small pieces, respectively. The two categories are separated depending on the diameter at a specific point on a tree or a log. However, the

threshold value varies from 0 to 35 cm (Cienciala et al., 2008). According to IPCC (2003), the border diameter is 10 cm. Harmon & Sexton (1996) found that below this diameter the decay rate increases exponentially, while above this diameter the decay rate decreases only slowly. Due to this fact, the decomposition process of coarse woody debris (CWD) can sometimes take up to 1,000 years (Feller, 2003) depending on wood characteristics (tree species, dimensions), climate characteristics (temperature and moisture, Woodall & Liknes, 2008) and the position on the ground (i.e. contact with the ground, Radtke et al., 2004). Since CWD persists a substantial time in the ecosystem, it is regarded as a more significant component of deadwood than fine woody detritus. Hence, most inventories do not account for fine woody debris and deal only with the components of coarse woody debris.
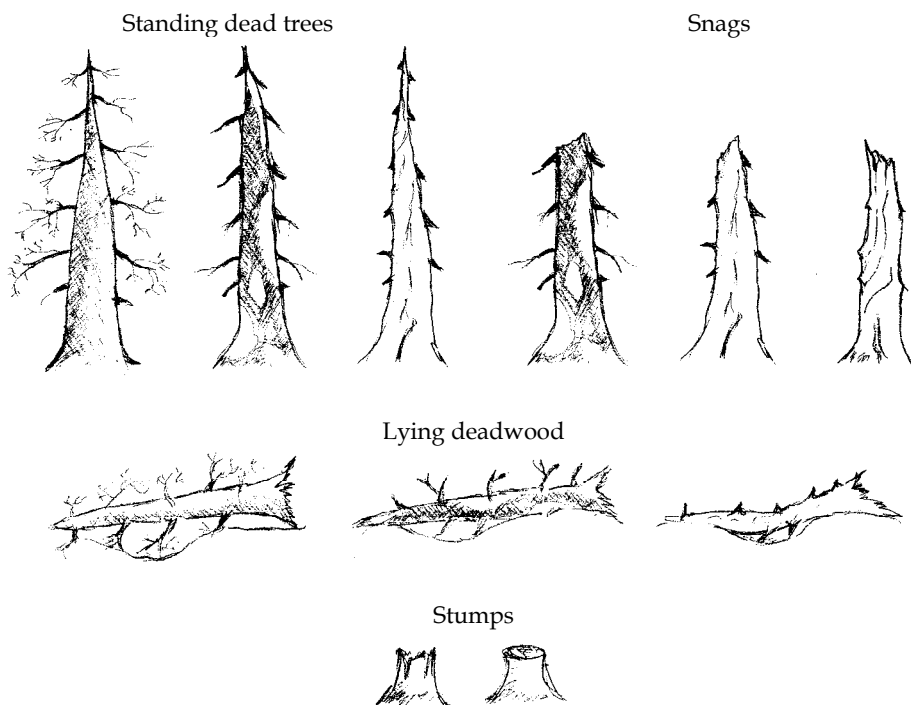
Standing dead trees   Snags

Lying deadwood

Stumps

Fig. 2. Types of aboveground deadwood.

3. Deadwood assessment

Nowadays, deadwood is assessed in many countries of the world within national inventories, and through various forest research activities. However, there is no accepted standard for the assessment of deadwood (Fridman & Walheim, 2000; Schuck et al., 2004; Stokland et al., 2004). A thorough analysis was performed by Schuck et al. (2004), who identified seven general deadwood attributes. From them, Rondeux & Sanchez (2009) selected three basic parameters: tree species, dimensions (diameter, height or length), and decay stage. Other attributes, such as cause of death, presence of cavities, or amount of bark left, are less frequently used (Rondeux & Sanchez, 2009).

3.1 Parameters of deadwood

3.1.1 Tree species

Tree species is important particularly because it determines the decay rate of deadwood (Rondeux & Sanchez, 2009) and the habitat qualities for colonising species (Schuck et al., 2004). For recently dead trees, the identification of tree species is quite easy, but as decomposition advances, the identification becomes more difficult (Rondeux & Sanchez, 2009; Stokland et al., 2004). The best criteria are bark surface, and wood structure (Stokland et al., 2004). In Scandinavia, the angle between the trunk and the branches is also used as an identification criterion for separating between Pinus sylvestris and Picea abies, or between coniferous and broadleaved species (Stokland et al., 2004). If a tree species or a genus is impossible to determine, it is recommended to distinguish between conifers/broadleaves and/or hardwood/softwood (Rondeux & Sanchez, 2009; Schuck et al., 2004; Stokland et al., 2004), as many colonising species show preferences for a certain tree species or a group of species (Stokland et al., 2004). From 16 examined tree genera, Quercus was found to have the highest number of specialists (58 species, Jonsell et al., 1998). However, almost all tree genera have some monophagous species, i.e. species restricted to a single tree genus (Jonsell et al., 1998). According to Stokland et al. (2004), only 10% of the colonising species are generalists that utilise both coniferous and broadleaved tree species. As the wood decays, the host range broadens (Jonsell et al., 1998). In the latest stage of decomposition, when it is clearly impossible to determine tree species or a group, deadwood is classified as "unindentified" (Rondeux & Sanchez, 2009; Stachura et al., 2007; Stokland et al., 2004).

3.1.2 Dimensions

Dimensions are necessary attributes to calculate approximate volume of deadwood (Stokland et al., 2004). They are also used to distinguish between individual types of deadwood, e.g. coarse and fine woody debris, or snags and stumps. According to Stokland et al. (2004), diameter is one of the most important biodiversity attributes of deadwood, since a majority of species colonising deadwood respond to its value. While some species prefer small diameters up to 20 cm, other species colonise only deadwood with diameters greater than 20 cm or even 40 cm. Only about 20% of the examined species were found to be generalists (Stokland et al., 2004).

As already mentioned, the variability of minimum threshold diameter between coarse and fine woody detritus is large. In the context of forest management dead wood with diameter of more than 6-7 cm is generally accepted as "deadwood" (Atici et al. 2008), while smaller material is considered of lesser importance (Colak, 2002). Some authors (e.g. Debeljak, 2006; Travaglini et al. 2007; Vandekerkhove et al. 2009) use minimum threshold 5 or 7 cm, which equals the threshold diameter for living trees. Other authors (e.g. Atici et al., 2008; Fridman & Walheim, 2000; Nordén et al., 2004) use the diameter limit 10 cm as suggested by Harmon & Sexton (1996). However, Vandekerkhove et al. (2009) showed that the differences in diameter thresholds did not significantly affect the results, and concluded that unlike stand density, deadwood volume is less affected by size thresholds.

The main attributes used for describing standing deadwood are diameter and height (Rondeux & Sanchez, 2009). In case of standing dead trees and snags with height 1.3 m or more, diameter at breast height is measured. In case of stumps and snags shorter than 1.3 m,

diameter at the level where the tree was cut or where the stem was broken off is measured (Travaglini et al., 2007). For lying deadwood, a diameter in the middle of the log (a so called mid diameter) and its length are the main attributes (Rondeux & Sanchez, 2009). Alternatively, diameters at the top and bottom ends of the log (i.e. top and basal diameter, respectively) can be measured in order to produce more precise volume calculations (Harmon & Sexton, 1996).

3.1.3 Decay stage

Decomposition is the process by which organic material is broken down into simpler forms of matter. If the decomposition is driven by physical and chemical processes, it is referred to as abiotic decomposition, while biotic decomposition is the degradation by living organisms, particularly microorganisms. It usually occurs in a number of sequential stages. As presented by Stokland et al. (2004), decay stage is an important quality influencing the associated species composition. In case of decay fungi, Veerkamp (2003) stated that it is the most important factor affecting their occurrence.

The decomposition of deadwood has been studied in many forests of the world (Bütler et al., 2007; Harmon et al., 2000; Jonsson, 2000; Krankina & Harmon, 1995; Kruys et al., 2002; Morelli et al., 2007; Næsset, 1999; Storaunet & Rolstand, 2002; Yatskov, 2001; etc.). The results of these studies showed that the rate/speed of decomposition of deadwood depends on a number of factors (Næsset, 1999), which can be divided into wood characteristics (tree species, dimensions) and site environmental factors (Radtke et al., 2004). Temperature and moisture seem to be the driving site parameters (Yin, 1999), but also the aspect of slope has an effect on the decomposition rate (Harmon et al., 1986). The contact of the deadwood with the ground is another important factor increasing the decay rate (Hytterborn & Packham, 1987, as cited in Næsset, 1999; Duvall & Grigal, 1999; Mattson et al., 1987).

Visual classification of deadwood is the most common approach of decomposition assessment (Bütler et al., 2007). The classification schemes generally distinguish several (3-7) decay stages (e.g. Holeksa, 2001; Lee et al., 1997; Maser et al., 1979; Næsset, 1999; Sollins, 1982). Each study defines its own class specification according to its objectives (Rondeux & Sanchez, 2009). The characterisation of decay stages/classes is usually based on the morphological features (log shape, wood texture, bark adherence, presence or absence of twigs and branches), hardness of the wood, and position with respect to the ground. The hardness of the wood, or the level of rottenness, is assessed by the depth a pushed knife penetrates the wood (Holeksa, 2001; Kuuluvainen et al., 2002; Rouvinen et al., 2005; Pasierbek et al., 2007). Other characteristics that have proven useful to distinguish decay classes include colour of wood, sloughing of wood, friability or crushability of wood (Harmon & Sexton, 1996). Some studies also use the presence of biological indicators (e.g. moss or plant cover, Holeksa, 2001), but Harmon & Sexton (1996) argue that they are of little value because they significantly vary even within a limited area.

Usually, the first decay class represents recently dead wood, which is least decayed with intact bark, present twigs and branches, round shape, smooth surface, intact texture, and the position elevated on support points. As the decay process proceeds the twigs, parts of branches and bark become traces to absent, wood becomes softer and fragmented, and the round shape becomes elliptical. The last decay class represents the most decomposed dead wood with no bark, twigs or branches, which is very soft, strongly fragmented and in contact with the ground along the whole length.

In order to quantify the decomposition process in a more objective way, it may be more straightforward to measure target variables. One method that involves ultrasonic measurements to characterize the wood quality of timber has been described by Sandoz (1989).

3.1.4 Volume, biomass, carbon

The volume of deadwood can either be calculated from the basic dimensions (diameter and height) or estimated on the base of the ocular judgement, which is the simplest and the most cost-effective, but a less accurate method. A thorough analysis of deadwood volume calculations is presented in Rondeux & Sanchez (2009). In general, the calculation of volume of individual standing and fallen dead trees follows the approaches applied to living trees (Rondeux & Sanchez, 2009). The most precise method is the volume equation derived for a particular species and region. Volume tables represent an easier, but a less precise approach (Šmelko, 2010).

In case of snags higher than 1.3 m, some authors (e.g. Travaglini & Chirici, 2006; Vacik et al., 2009) use the same approaches as for the living trees multiplied by a reduction factor representing the reduction of the tree height due to the top breakdown. Other studies approximate the volume of snags by common geometric solids (cylinders, cones, paraboloids), which the wood pieces resemble most (Rondeux & Sanchez, 2009). For example, Vandekerkhove et al. (2009) used the formulas of truncated cones. Merganičová & Merganič (2008) used an integral equation based on the models of stem shape derived by Petráš (1986, 1989, 1990).

Logs, i.e. lying deadwood pieces, usually resemble cylinders. There are three possibilities to calculate their volume depending on which diameters were measured. If only a mid diameter was measured, their volume is calculated using Huber´s formula. In case, top and bottom diameters are known, Smalian´s formula is used. Occasionally, all three diameters (top, middle, and bottom) are measured. In such cases, Newton´s formula can be applied. Concerning the question about the ideal formula to estimate log volume, Harmon & Sexton (1996) concluded that on average, all the formulae presented above should give satisfactory results. For individual logs, Newton's formula had the smallest average deviation from the "true" volume, but none of the formulae were biased (Harmon & Sexton, 1996). The volume of stumps is usually calculated using the formula of cylinder (e.g. Rouvinen et al., 2005).

Belowground volume of deadwood is usually omitted from the studies. Debeljak (2006) presented a method for the calculation of the belowground quantity of coarse woody debris based on the aboveground volume, ratio between the total volume to the root system volume, and the decay stage. Similarly, fine woody debris is only rarely included in the analyses.

Most of the above stated approaches dealt with the volume of individual deadwood pieces. To obtain a value representing the whole stand, the volumes of all occurring types of deadwood (dead trees, snag, logs, stumps) are summed up and converted to hectare values. The stand volumes of deadwood are used to compare different forests, regions, countries, and to evaluate the level of biodiversity, naturalness, or sustainability.

However, volume is not the best indicator if nutrient cycling and/or carbon sequestration are of primary interests, because during the decomposition process woody debris looses not only its volume, but also its mass and density (Coomes et al., 2002; Harmon et al., 2000; Krankina & Harmon, 1995). In such cases, biomass and carbon stock are estimated from

volume. Carbon storage in wood is obtained by converting the volume mass into the amount of carbon stored in deadwood. For this conversion, carbon content in wood and wood density need to be known. Usually, carbon fraction in wood is approximated 50% of the woody dry mass (Coomes et al., 2002). Weiss et al. (2000) published more precise values for individual tree species of Central Europe. According to these authors, carbon content in Norway spruce wood is 50.1%, while in European beech 48.6%. This fraction remains stable during the whole decomposition process of deadwood (Bütler et al., 2007).

Unlike carbon fraction in wood, wood density decreases as wood decays (Harmon et al., 2000). While basic wood density of Norway spruce living trees fluctuates around 0.43 g cm⁻³ (Bütler et al., 2007; Morelli et al., 2007, Weiss et al., 2000), the average density of the most decayed Norway spruce deadwood is only 0.138 g cm⁻³ (Merganičová & Merganič, 2010). This is a significant reduction of wood density over the course of decomposition, which needs to be taken into account in the carbon stock studies. Merganičová & Merganič (2010) presented that when the volume of coarse woody debris was converted to carbon stocks using the basic wood density of fresh wood (i.e. 0.43 g cm⁻³), deadwood carbon stocks were overestimated by 40% or more.

3.2 Deadwood inventory

Initially, information about deadwood was collected to address wildlife habitat issues (Bütler, 2003). Nowadays, deadwood is considered relevant for a number of different issues including nature conservation, forest certification, sustainable forest management, carbon sequestration, etc. Hence, deadwood is now assessed in many parts of the world within national forest inventories and various research activities. However, no harmonised methodology for deadwood inventory exists, as the objectives and the needs differ between the studies (Rondeux & Sanchez, 2009). In spite of these differences, simple, fast and accurate methods are required for both research and management purposes (Bütler, 2003).

In general, the survey can be accomplished either in the whole area of interest, or only on a portion of the given area. Although complete enumeration can provide us with the information about each individual, in large populations, such as forests, this survey is usually not economically and practically feasible. Hence, complete field inventory has been applied very scarcely, e.g. for the repeated measurements of virgin forests in the Czech republic (Vrška et al., 2001a, 2001b, 2001c), or to compare different assessment methods (e.g. Bütler, 2003). Because of high time and cost demands, sampling is often applied instead, while its main condition is that the selected sample represents the whole population. As Shiver & Borders (1996) pointed out, in most cases sampling can be more reliable than complete inventory, because more time can be taken to measurements, while sampling error could be kept small. There exist a great number of publications devoted to sampling techniques in general, e.g. Cochran (1977), Hush et al. (2003), Kish (1995), Shiver & Borders (1996), Schreuder et al. (1993), Šmelko (1985), Thompson (2002), Zöhrer (1980), etc., presenting different sampling designs from simple random sampling, through systematic and stratified sampling, up to multi-stage or multi-phase sampling designs. Deadwood sampling methods present specific characteristics with regard to the spatial distribution and the variability of deadwood components (Rondeux & Sanchez, 2009). As already mentioned, deadwood consists of different types (standing/lying, aboveground/belowground, coarse/fine woody debris) several of which would ideally require their own survey method. Due to this complexity, the majority of studies usually account only for the selected

components of deadwood. For example, Marage & Lemperiere (2005) studied standing dead trees only. Most often the aboveground coarse woody debris is the subject of interest, while belowground deadwood is conventionally excluded because its assessment and quantification is difficult (Rondeux & Sanchez, 2009).

Standing deadwood is usually inventoried with the same methodology as living trees (Rondeux & Sanchez, 2009). The common approach is the plot-based sampling, while the plots can either be of fixed or variable area. An example of plots with variable area is when the plots are selected depending on a certain pre-defined number of trees to be included, e.g. the optimisation study of Šmelko (1968) proposed to measure 20-25 trees. In some cases, a set of concentric circles is used (Oehmichen, 2007; Šmelko & Merganič, 2008). Bütler (2003) and Vacik et al. (2009) applied the Bitterlich relascope point sampling, which uses a fixed angle of sight to select the trees to be assessed.

Lying deadwood can also be assessed on the same sample plots as living trees or standing deadwood. The only exception is the Bitterlich sampling method, which cannot be applied to downed deadwood directly (Vacik et al., 2009). In case of plot-based sampling, a common approach is to inventory only the deadwood inside the plot, i.e. if the log crosses the plot border, the part outside the plot is not accounted for in the inventory (Oehmichen, 2007). The second widely used approach is the line intersect sampling firstly presented by Warren & Olsen (1964) and Wagner (1968) for the inventory of logging waste and fuel wood, respectively. The principle of the method is that only the deadwood that crosses the line/transect is inventoried.

Both plot-based and line-based sampling techniques have some advantages and disadvantages. Line sampling is fast and accurate (Harmon & Sexton, 1996), easy to use, more time efficient and more economical than plot-based approach (Oehmichen, 2007). However, plot-based sampling is applicable to all types of deadwood, while line intersect method includes only lying deadwood. Hence, if this method is to be used for the deadwood assessment, it must be coupled with another method to consider standing deadwood. Additionally, Oehmichen (2007) and Rondeux & Sanchez (2009) stated that line intersect sampling is not suitable for long-term monitoring.
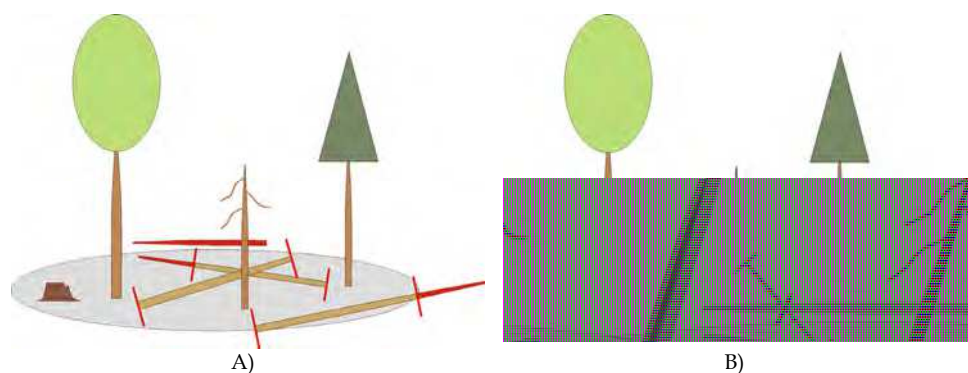

A)   B)

Fig. 3. Assessment of coarse woody debris using fixed-area (A) and line intersection (B) sampling techniques. Red colour indicates the elements of coarse woody debris that are not inventoried with the particular method.

Apart from the measurement-based inventory methods, the approach of visual estimation is also used, particularly for the inventory of fine woody debris, as its measurement would be too time consuming. With the visual assessment we can either directly estimate the volume of fine woody debris. However, more frequently other parameters, from which the volume is calculated, are estimated, e.g. average diameter and length (Rondeux & Sanchez, 2009), and the coverage of the plot by fine woody fractions (Šmelko et al., 2006; Šmelko & Merganič, 2008; Šmelko, 2010).

The methods presented so far are field inventory techniques. With the progress of modern technology, new approaches based on remote sensing are promising for coarse deadwood inventory. Infrared aerial photos are suitable for mapping and quantifying of standing deadwood (dead trees and snags) (Bütler, 2003; Bütler & Schlaepfer, 2004), but lying deadwood is not possible to map unless their resolution is 20 cm (Frei et al., 2003, as cited in Oehmichen, 2007). Pesonen et al. (2008) and Vehmas et al. (2009) used airborne laser scanning to assess coarse woody debris characteristics and stated that this approach can be used for the preliminary mapping of forests with large amounts of downed deadwood.

4. Functions of deadwood in forest ecosystems

4.1 Biotope

A great number of different plant and animal species have been associated with deadwood as a space for their lives or the parts of their lives. Over the last decades, the scientific studies have shown that deadwood provides valuable habitats for lichens, bryophytes, fungi, invertebrates, small vertebrates, birds, and mammals (Humphrey et al., 2004). Although the exact numbers differ between regions and studies, in general it has been assumed that around 25% of species occurring in forests are dependent on decaying wood (Schuck et al., 2004). The same number was reported by Siitonen (2001) and Stokland et al. (2003) for Scandinavia.

For saproxylic organisms, dead and dying trees and their parts are the key elements of their life (Davies et al., 2008; Grove, 2002; Lonsdale et al., 2008; Zhou et al., 2007). The group of saproxylic species is the most diverse group in forest ecosystems (Schuck et al., 2004), as it includes all species that depend on deadwood during some part of their life, or upon other saproxylics (Speight, 1989). The main saproxylic taxa are fungi (Ferris et al., 2000; Pouska et al., 2010; Siitonen, 2001), bryophytes (Kruys et al., 1999; Kushnevskaya et al., 2007; Odor & Standovar, 2001; Zielonka & Piatek, 2004), lichens (Kushnevskaya et al., 2007), arthropods such as beetles (Davies et al., 2008; Jonsell & Nordlander, 2002; Persiani et al., 2010), and birds (Bütler et al., 2004). From other groups with a smaller number of saproxylic species we can name mammals such as bats and dormice (Maser & Trappe, 1984), amphibians (DeMaynadier & Hunter, 1995), and moluscs (Kappes et al., 2009).

For other species, deadwood is a source of food and/or construction materials, a nesting and/or breeding site, a shelter, and a hiding place (Bütler, 2003; Debeljak, 2006). The tunnels left after wood-destroying insects can be used as a hiding place for other insects, e.g. wasps (Ehnstrom, 2001). Deadwood can also be used as a lookout post by mammals, e.g. squirrels (Bütler, 2003), or lynx (Bobiec et al., 2005).

4.2 Substrate

Coarse downed deadwood represents favourable environment for the natural regeneration of plant species starting from moss, ferns, and herbs (Franklin et al., 1987; Harmon et al., 1986; Radu, 2007). It is also a primary site to be colonised by fungi and an important seedbed for regenerating tree species. In some forests, the regeneration of tree species is exclusively dependent on the presence of deadwood (Nakagawa et al., 2001; Narukawa & Yamamoto, 2002; Narukawa et al., 2003; Takahashi et al., 2000). In some cases, tree seedlings occur only on the logs of the same tree species (Hofgaard, 1993), while in other cases they colonise the logs of other tree species (Harmon & Franklin, 1989). On deadwood, seedlings are provided with better temperature and moisture conditions (Mai, 1999). Due to these qualities, deadwood is an important rooting substrate particularly in cool climate and severe conditions of boreal (Harmon & Franklin, 1989) and mountain forests (Szewczyk & Szwagrzyk, 1991; Vorčák et al., 2005). Lepšová (2001) and Jaloviar et al. (2008) reported that the root system of the seedlings growing on woody debris was better developed. In ecosystems with abundant herb layer, the regeneration established on such "nurse logs" (Harmon et al., 1986) is favoured against the competing plants (Mai, 1999). However, not all coarse woody debris is a suitable place for regeneration. The suitability of downed deadwood for the regeneration depends on its qualitative parameters, mainly the decay stage, which is closely coupled to other characteristics (moisture, nutrient content). More decayed wood is more appropriate than fresh or slightly decayed deadwood (Merganič et al., 2003).
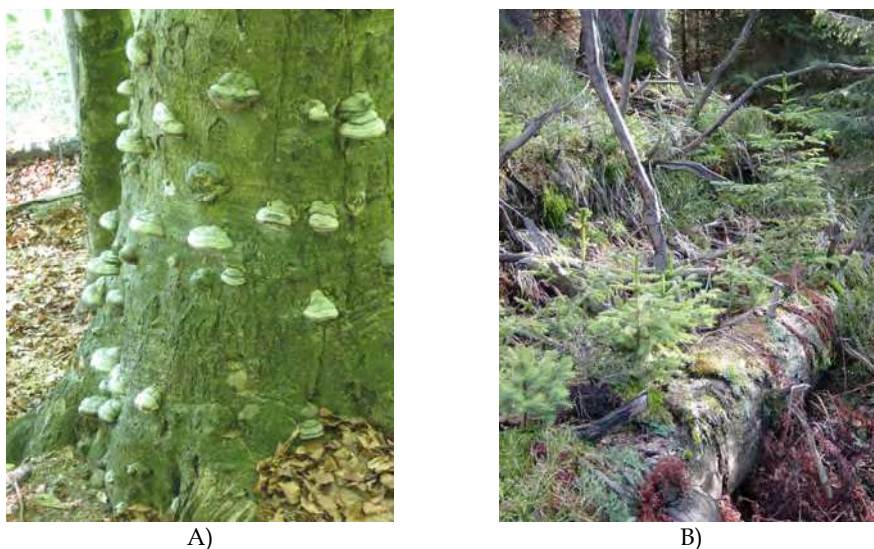

| A) | B) |

Fig. 4. Deadwood as biotope for saproxylic fungi (A) and substrate for new generation (B), photo by J. Vorčák.

4.3 Nutrient source

Deadwood significantly affects the flow of mass, energy and nutrients in ecosystems. The accumulation and decomposition of organic material on soil surface and in soil is closely

coupled to nutrient cycling (Green et al., 1993). Although the relative concentration of nutrients in wood and bark is low, due to the large biomass amount of deadwood it is the main source of nutrients and carbon in forest ecosystems (Caza, 1993; Harmon et al., 1986). Nutrients are released from deadwood slowly over a long time; hence deadwood acts as a natural fertiliser (Holub et al., 2001; Hruška & Cienciala, 2002; Janisch & Harmon, 2001; Mackensen & Bauhus, 2003; Turner et al., 1995). Stevens (1997) reported that coarse woody debris is a nutrient source for more than 100 years. The release of nutrients can be performed by several different ways. Fungi and mosses growing on the surface take nutrients from deadwood, and hence, create a so-called zone of active nutrient cycling (Nadkarni & Matelson, 1992). The flow of nutrients runs through the mycelia of wood decomposing fungi (Zimmerman et al., 1995) as well as through the mycelia of ectomycorrhizal fungi (Lepšová, 2001). It is assumed that the colonisation of deadwood by fungi and microbes is one of the main phases of nutrient cycling (Caza, 1993). The microorganisms and wood-decomposing fungi decompose organic molecules of wood, and thus release the nutrients for plants (Stevens, 1997). All ways of nutrient release are directly or indirectly coupled to the processes causing wood decay. In addition, deadwood is also an important resource of water, especially in dry periods (Harmon & Sexton, 1995; Pichler et al., 2011).

5. Importance of deadwood

5.1 Productivity

The presence of deadwood in forest ecosystems increases their productivity (Marra & Edmonds, 1994; Mcminn & Crossley, 1993). Debeljak (2006) compared managed and virgin forest stands and found that the maximum tree height was significantly lower in the managed stands which may indicate the reduction of forest productivity due to the reduction of coarse woody debris.

5.2 Biodiversity

Since deadwood has been recognised as a habitat of great importance for many species of forest ecosystems, it is considered to be a key element of biodiversity in forests. In many cases, deadwood is associated with relict, rare and protected species (Radu, 2007), and therefore, it is regarded as a key feature for the preservation of many threatened species (Ranius et al., 2003). The recognition of the deadwood importance for biodiversity has led to the incorporation of its quantitative parameters in biodiversity monitoring programmes (Humphrey et al., 2004), e.g. the European Environmental Agency includes deadwood as one of 15 core biodiversity indicators (Kristensen, 2003). The results of the different studies suggest, that the importance of deadwood and its individual parameters differs between the sites and cannot be generalised. According to Humphrey et al. (2004), coarse woody debris is an important biodiversity indicator in conifer-dominated forests in the Atlantic and Boreal biogeographical regions, but is less applicable to Mediterranean forests.

The biological importance of deadwood depends on several factors, in particular on tree species, dimension, vertical and horizontal position, decay stage, and micro-environmental conditions (Radu, 2007). From all deadwood characteristics, the amount of deadwood is usually taken as an indicator of biodiversity (Stokland et al., 2004; Vandekerkhove et al., 2009). A higher amount of deadwood in forests increases the number, and the density of

species, and hence, species richness, because higher deadwood amount means greater surface and area in forests, and hence, its higher availability for potential users (Müller & Bütler, 2010). This is in accordance with the island theory (Cook et al., 2002) according to which we can expect higher number of species in a unit with a larger "island". Secondly, larger surface means greater possibilities of its differentiation (Müller & Bütler, 2010) providing species with a greater variability of habitats.

Several studies detected the correlation of species richness to deadwood amount (Müller & Bussler, 2008; Müller & Bütler, 2010). It is widely agreed that 20-30 m^3·ha^{-1} is the required amount that can safeguard the complete spectrum of deadwood-depending species (Angelstam et al., 2003; Humphrey et al., 2004; Siitonen, 2001; Vandekerkhove et al., 2009), although some authors presented higher values. For example, according to Müller & Bussler (2008), the critical threshold for saproxylic Coleoptera is between 40 and 60 m^3·ha^{-1}. Other studies argued that for some taxa the diversity of deadwood components, and its continuity in space and time is a more important feature than its amount (Heilmann-Clausen & Christensen, 2004; Schiegg, 2000a; Similä et al. 2003). Hence, for biodiversity conservation it is also important to balance the proportions of individual deadwood types and decay stages (Hagan & Grove, 1999), as each type represents quite different habitats suitable for different species.

5.3 Naturalness

Deadwood characteristics are also common attributes used for assessing forest naturalness (Laarmann et al., 2009; Winter et al., 2010), since the differences in deadwood between managed and unmanaged forests are in most cases notable (Kirby et al., 1998; Liira et al., 2007). In general, the amount of deadwood is lower in managed in stands than the stands left to self-development (Rahman et al., 2008; Rondeux & Sanchez, 2009; Travaglini & Chirici, 2006), because most of large-sized wood is extracted from the forest. Therefore, to determine the level of naturalness of forest ecosystems, the amount of coarse woody debris has become an important indicator (Rahman et al., 2008). However, for the proper application of deadwood as an indicator, reference values representing the "natural" state are needed. Such values can be obtained from natural unmanaged forests (virgin/old-growth forests) (Hahn & Christensen, 2004; Humphrey et al., 2004). However, when using the reference values it must be considered that the volume of deadwood varies considerably among forest sites. While in North America the volume of coarse woody debris in old-growth forests may exceed 1,000 m^3·ha^{-1} (Harmon et al., 1986), in Europe the average values between 40 and 200 m^3·ha^{-1} have been reported (Albrecht, 1991; Christensen et al., 2005; Hort & Vrška, 1999; Karjalainen et al., 2002; Siitonen et al., 2000; Vallauri et al., 2003; Vandekerkhove et al., 2009). Larger values (more than 400 m^3·ha^{-1}) have been found in virgin forests of Central Europe, e.g. Slovakia (Saniga and Schütz, 2001), Poland (Bobiec, 2002), Slovenia (Debeljak, 1999, 2006). Even in Europe, there is a large variability of deadwood accumulation, when northern boreal and southern Mediterranean forests are characterised by a lower deadwood amount than Central European mixed forest types (Hahn & Christensen, 2004).

Large amount of deadwood does not necessarily indicate the high level of naturalness of forest ecosystems (Laarman et al., 2009; Marage & Lemperiere, 2005; Rouvinen et al., 2005; Pasierbek et al., 2007), particularly in cases when it is the result of the accelerated breakdown of forest stands (Jankovský et al., 2004) due to disturbances. The analysis of Laarman et al. (2009) reported that the spatial distribution of deadwood, proportion of

recent mortality and the causes of mortality seem to be better indicators. Marage & Lemperiere (2005) revealed that the differences between the managed and unmanaged forest stands were only in the category of standing dead trees, as in the managed stands the trees are extracted before they reach their maximum diameter. Hence, deadwood is an appropriate indicator of naturalness only if the additional information about its components, decay stages, etc. is also available (Liira & Sepp, 2009; Rondeux & Sanchez, 2009).

5.4 Geomorphology

Mechanical and physical qualities of large-sized deadwood have a significant influence on the geomorphology of forest soils and small watercourses in forest ecosystems (Stevens, 1997). On slopes, coarse woody debris significantly contributes to slope and soil surface stability. Fallen logs prevent or slow down soil erosion and surface water runoff (Kraigher et al., 2002; Stevens, 1997), and act as barriers for rock fall and avalanches (Kupferschmidt et al., 2003).

6. Factors influencing deadwood pool in forest ecosystems

Deadwood is the result of the influence of various abiotic and biotic factors on individual trees or forest stands. The quantity of deadwood and its decomposition in a particular forest ecosystem depends on many intrinsic and extrinsic factors that drive the input of deadwood and its decomposition process. Intrinsic factors include deadwood type, dimensions, and tree genus that determines basic tree and wood characteristics, while extrinsic factors include climate and site conditions, and disturbances.

Tree species can predetermine the mortality pattern and subsequently the accumulation and decomposition of deadwood. Species with a shallow root system, e.g. Norway spruce, are susceptible to uprooting, while deep-rooted species usually suffer from breakdown. However, under favourable climate and soil conditions, this may not hold, as e.g. in mountain spruce forests of Babia hora Holeksa (2001) detected that the snags were dominant over the uprooted trees, whose proportion was much lower than in other temperate and boreal spruce forests.

The rate of deadwood decay depends on the chemical composition of wood, which is specific for each tree species. Some tree species are decay resistant, for example oak or pine (Radu, 2007). Softwood species, e.g. willow, birch, and poplar, have a much shorter period of decomposition (Radu, 2007). The resistance of deadwood depends on the content of extractives (polyphenols, waxes, oils, resins, gums, tannins) in the heartwood, which are toxic to most decay fungi and some insects, and hence slower the decomposition process.

However, the decay resistance of a particular species may vary greatly depending on the dimensions and site conditions. The length of the decomposition process is positively correlated with deadwood diameter. The turnover of fine dead woody debris is fast (Stevens, 1997), while its decomposition rate increases exponentially with decreasing diameter (Harmon & Sexton, 1996). The differences in decay rate are also between standing and lying deadwood. The decay of snags is slower than the decay of logs because of lower wood moisture (Kupferschmidt et al., 2003). Snag diameter has also a positive influence on the time length the snag stands (Everett et al., 1999; Morrison & Raphael, 1993, as cited in Bütler, 2003).

From site conditions, temperature and moisture seem to be the driving factors. In warm, moist environments decay rates are higher, because such conditions favour microbial and fungal growth (Yin, 1999). This is evident in the analysis of deadwood volume along the elevation gradient. According to MCPFE (2007), the lowest amount of deadwood is in the forests situated at the lowest elevations. As elevation increases, accumulated deadwood volume enlarges. This increasing trend with elevation was also observed in the national analysis in Slovakia (Merganič et al., 2011), when at the lowest elevations the authors reported only 10 $m^3 \cdot ha^{-1}$, while under the timber line the deadwood volume was around 100 $m^3 \cdot ha^{-1}$. Similarly, Kühnel (1999) reported that in mountain forests the amount of deadwood is three times higher than in lowlands.

6.1 Disturbances

In natural forests deadwood originates from tree mortality, which is either the result of inter-tree competition or senescence processes, or it is caused by natural disturbances, which can differ in terms of quality and quantity (Rahman et al., 2008). Disturbances can be driven by abiotic (wind, fire) and/or biotic factors (insect outbreak). Windthrow, icebreak, insect and fungal attacks leave various amounts of deadwood in the forest, while during fire disturbances deadwood is immediately consumed (Hahn & Christensen, 2004). The disturbance factors vary in intensity and scale leading to a patchy distribution of deadwood at the stand and landscape levels (Humphrey et al., 2004). Small-scale disturbances cause the death of individual trees or small groups of trees, while large-scale disturbances affect the whole ecosystem (Korpeľ, 1995).

A)   B)

Fig. 5. Large-scale disturbances caused by windthrow (A) and insect outbreak (B).

Small-scale events occur frequently and hence provide a continuous supply of deadwood (Rahman et al., 2008). Due to this, in forests following a so-called small cycle deadwood of different size and decay stages can be found (Korpeľ, 1995; Saniga & Schütz, 2001). On the landscape level, the deadwood pool is relatively stable, and the differences are obvious only on a small scale between the developmental stages. The highest amount of deadwood occurs in breakdown developmental stages, while the lowest amount is in the stage of maturity (Merganičová et al., 2004; Merganičová & Merganič, 2010).

In contrast, large-scale disturbances cause abrupt changes of the whole ecosystem, which result in high deadwood inputs at the time of the event. At this stage, these ecosystems may attain higher amounts of deadwood than the forests developing in a small cycle (Rahman et al., 2008; Šebeň et al., 2009). However, in the following successional stages, deadwood input is minimal, and the total amount of deadwood declines (Rahman et al., 2008).

6.2 Forest management

Apart from the natural factors discussed so far, a man with its activities also affects deadwood in forest ecosystems either directly through forest management or indirectly by e.g. air pollution (Debeljak, 2006). While the first forms of human utilisation of wood, e.g. domestic use of wood, had apparently only a slight influence (Rouvinen et al., 2005), with the increasing human population, human influence has become more intensive and widespread (Björn, 1999, as cited in Rouvinen et al., 2005). Nowadays, it is generally agreed that forest management has a negative effect on deadwood amount and deadwood components (Atici et al., 2008). Dead, damaged and weakened trees are often removed from the forest during harvesting operations (Bütler, 2003). Thinnings reduce deadwood inputs from natural mortality. Short rotation time limits the presence of large dead trees (Bütler, 2003; Debeljak, 2006; Marage & Lemperiere, 2005), because trees are harvested before they reach their maximum diameter (Atici et al., 2008). After natural disturbances, such as windthrow or insect outbreak, dead trees are harvested in salvage logging (Bütler, 2003). The effect of management on deadwood is linked with the accessibility of harvesting areas. Bütler (2003) found a significant negative relationship between road density and deadwood amounts in Switzerland. Pasierbek et al. (2007) detected more deadwood on the sites which were situated far from the settlements.

The current amount of aboveground deadwood in managed forest is very low. According to Nilsson et al. (2002), before human exploitation common deadwood amount in European forests was 130-150 $m^3 \cdot ha^{-1}$, nowadays the values range from 1 to 23 $m^3 \cdot ha^{-1}$ (MCPFE, 2007). Usually, the average amount of aboveground deadwood does not exceed 10 $m^3 \cdot ha^{-1}$ (FAO, 2000; Fridman & Walheim, 2000; Christensen et al., 2005). In some cases, it does not even reach 5 $m^3 \cdot ha^{-1}$ (Albrecht, 1991; Smykala, 1992; Schmitt, 1992; Vallauri et al., 2009). In addition, deadwood in managed forests typically consists of fine woody debris (small twigs and branches) and short stumps (Atici et al., 2008). A large, but often a forgotten part of woody debris in managed stands may be belowground deadwood originating from root systems of cut trees (Debeljak, 2006). This author presented that the proportion of belowground coarse woody debris in managed forests is significantly higher than in virgin forests. However, this type of deadwood is buried, and therefore not available to all saproxylic species, e.g. birds.

Therefore, in the interests of sustainable forestry and biodiversity conservation the efforts are being made to increase the levels of deadwood in managed forests (Atici et al., 2008). There exist a great number of publications that deal with the question how much deadwood should be left in a forest. However, the variation of the recommended values is quite large. Older studies suggest at least 3 $m^3 \cdot ha^{-1}$ (Utschik, 1991) or 5-10 $m^3 \cdot ha^{-1}$ (Ammer, 1991), which is 1-2% of the total volume of the stand. In more recent studies the suggested values are higher and fluctuate between 15 and 30 $m^3 \cdot ha^{-1}$ (Bütler & Schlaepfer, 2004; Colak, 2002; Jankovský et al., 2004), or 5-10% of the total stand volume (Bütler & Schlaepfer, 2004;

Jedicke, 1995; Möller, 1994; Vandekerkhove et al., 2009). According to Vandekerkhove et al. (2009), the minimum amount of deadwood should secure the existence of the whole spectrum of saproxylic species. The works dealing with their populations suggest 40 m³ ·ha⁻¹ to be the threshold value, when the diversity of saproxylic communities is comparable with the diversity in virgin forests (Haase et al., 1998; Kirby et al., 1998; Müller & Bussler, 2008). It is clear that very small values are too low to be important for nature conservation (Scherzinger, 1996) or biodiversity. Considering the large variation in the values of deadwood from natural forests, which are references for management, no universal value valid throughout the world exists (Jankovský et al., 2004). The guidelines and recommendations should be given for more homogeneous groups, e.g. individual forest types (Hahn & Christensen, 2004). The consensus should also be found between gains and losses (Atici et al., 2008).

7. Conclusion

Nowadays it is generally accepted that deadwood plays an important role in ecosystem dynamics. In this chapter we presented the synthesis of existing knowledge about deadwood including its assessment, evaluation, and factors influencing deadwood occurrence and dynamics. Although less than one decade ago, the information about the decay rates of deadwood in Europe was almost completely missing, this gap is currently being filled. Addressing the full spectrum of processes within forest ecosystems, in which deadwood occurs, we implied to coherently analyse its importance for sustainable forest management and issues closely coupled, e.g. biodiversity, naturalness. While the importance of deadwood for biodiversity has been thoroughly studied, less information is available about the relationship between deadwood and stand productivity and geomorphology. Future research should focus more on investigating belowground component of deadwood, which is currently usually not accounted for in the inventories. For forest management, more specific guidelines with regard to forest type and/or region would be helpful to maintain sufficient amount of deadwood for biodiversity preservation.

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9. References

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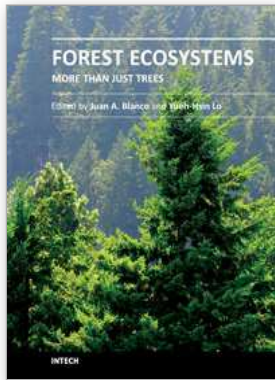
Forest Ecosystems - More than Just Trees

Edited by Dr Juan A. Blanco

The common idea for many people is that forests are just a collection of trees. However, they are much more than that. They are a complex, functional system of interacting and often interdependent biological, physical, and chemical components, the biological part of which has evolved to perpetuate itself. This complexity produces combinations of climate, soils, trees and plant species unique to each site, resulting in hundreds of different forest types around the world. Logically, trees are an important component for the research in forest ecosystems, but the wide variety of other life forms and abiotic components in most forests means that other elements, such as wildlife or soil nutrients, should also be the focal point in ecological studies and management plans to be carried out in forest ecosystems. In this book, the readers can find the latest research related to forest ecosystems but with a different twist. The research described here is not just on trees and is focused on the other components, structures and functions that are usually overshadowed by the focus on trees, but are equally important to maintain the diversity, function and services provided by forests. The first section of this book explores the structure and biodiversity of forest ecosystems, whereas the second section reviews the research done on ecosystem structure and functioning. The third and last section explores the issues related to forest management as an ecosystem-level activity, all of them from the perspective of the �other� parts of a forest.

How to reference

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