# **Czech University of Life Sciences Prague**

Faculty of Forestry and Wood Sciences Department of Silviculture



# Structure of the natural spruce mountain forests in the selected localities in Slovakia

Struktura původního horského smrkového lesa na vybraných lokalitách na Slovensku.

Diploma Thesis

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# Declaration

I hereby declare that I have formulated the thesis Structure of the natural spruce mountain forests in the selected localities in Slovakia independently under the supervision of doc. Ing. Miroslav Svoboda, Ph.D. and that I have used only the sources listed in References.

I am aware, that by presenting the thesis I agree with its release in accordance with Act No. 111/1998 Coll., on universities, as amended, regardless of the outcome of the thesis defence.

In Prague on

Michal Synek

Prohlašuji, že jsem diplomovou práci na téma Structure of the natural spruce mountain forests in the selected localities in Slovakia vypracoval samostatně pod vedením doc. Ing. Miroslava Svobody, Ph.D. a použil jen prameny, které uvádím v seznamu použitých zdrojů.

Jsem si vědom, že zveřejněním diplomové práce souhlasím s jejím zveřejněním dle zákona č. 111/1998 Sb. o vysokých školách v platném znění, a to bez ohledu na výsledek její obhajoby.

V Praze dne

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## Abstract

Natural mountain old-growth Norway spruce (Picea abies (L.) Karst.) forests have recently become an important subject in various ecological, biological and social studies. Studies on structure and dynamics of natural forest are of high importance since they provide an important guidance for forest managers and decision makers. Aim of this thesis is to collect data and on their basis describe structural variability and dynamics in the natural mountain spruce forest. Study was conducted in the Tatra National Park and cover two valleys with 16 plots each (total 1790 trees). Statistical analysis was applied to prove or reject the hyphotheses regarding dependence between structural parameters (e.g. living and dead standing trees, coarse woody debris, regeneration). The decreasing numbers of large trees in more dense stands, importance of dead wood volume for spruce regeneration and preference among available substrates among spruce regeneration (particularly in favor of dead wood) were proven significant. However, no significance was proven for change of stand density along altitudinal gradient. Most trends were well fitting in generally observed patterns but some, for example density of regeneration with respect to elevation, are not reflecting published informations. The importance of scale for serious part of the results is apparent too. Via comparison with other studies, which often involved different analyses, disturbance regimes leading to particular observed structures were considered. The observed structures seem to be following the patterns described as results of intermediate disturbance regimes. On larger scales the diameter distribution curve is resembling the shape of this curve as described for selection forest.

# Key words:

Norway spruce, Picea abies, stand structure, disturbances.

# Abstrakt

Původní horské smrkové (Picea abies (L.) Karst.) lesy se v poslední době stávají cílem různých ekologických biologických i sociálních studií. Studie týkající struktury a dynamiky těchto porostů mají značný význam, protože mohou poskytnout cenné informace použitelné v lesním hospodářství. Cílem této práce je sběr dat a na jejich základě popis variability a dynamiky přirozených horských smrkových lesů. Sběr dat byl proveden v Tatranském Národním Parku, kde bylo ve dvou dolinách zřízeno 32 výzkumých ploch (16 v každé, celkem 1790 měřených stromů). Statistické metody byly následně použity k potvrzení či vyvrácení hypotetických závislostí mezi různými strukturními parametry (např. množství živých stromů a souší, ležícího mrtvého dřeva, přirozené obnovy). Jako statisticky významný byl potvrzen pokles množství mohutných stromů v hustších porostech, význam mrtvého dřeva pro obnovu smrku a výrazná nerovnováha obnovy smrku na různých substrátech (ve prospěch ležícího mrtvého dřeva). Statisticky neprůkazná se ukazuje změna hustoty porostu v závislosti na nadmořské výšce. Většina trendů poměrně dobře odpovídá obecně pozorováným vzorům. Některé souvislosti, například četnost obnovy s měnící se nadmořskou výškou, neodpovídají dříve publikovaným informacím. Zjevnou se potvrdila také potřeba hodnotit různé souvislosti vždy s ohledem na měřítko. Porovnáním s jinými studiemi, které často použily také jiných metod a analýz, byly zvažovány disturbance a jejich režimy, které by mohly vést ke vzniku pozorovaných struktur. Struktura porostů na sledovaném území, zdá se, odpovídá vzorcům popisovaným jako důsledek intermediátních (středně silných a rozsáhlých a v obou těchto faktorech značně proměnlivých) disturbancí. Ve větším měřítku křivka skladby porostu podle tloušťkových stupňů poměrně dobře reflektuje tvar této křivky ve výběrném lese.

## Klíčová slova:

Smrk ztepilý, Picea abies, struktura porostu, disturbance

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# List of abbreviations used in the text

- BA Basal area, area of cross-section of tree stem.
- CWD Coarse Woody Debris, lying dead wood with diameter over 10cm.
- DBH Diameter at Breast Height, diameter measured at 1.3m above ground.
- NNR National Nature Reserve, smaller scale strictly protected area.
- NP National Park, large scale strictly protected area.
- NPR Národná Prírodná Rezervácia, Slovakian equivalent for National Nature Reserve, smaller scale strictly protected area.

# 1 Introduction

Even though in last decades the protection of natural or pristine forests has gained increased attention and support these stands are scarce. So are stands which were affected by human activity in the past but were given extensive time period to recover and possibly return to a structure closely resembling that of never-managed forests, oldgrowth forests. Observation of both these types of stands can provide important information not only about natural processes and structures but also about the effect of their modification or absence in managed stands. Therefore study of natural or oldgrowth stands should be of hight interest for ecologists just as much as for foresters. Even more since the focus of this thesis are old-growth mountain Norway spruce (Picea abies) stands and it is almost needless to note how important and common are spruce stands in central European region. Data were collected about wide spectrum of stand characteristics and they should serve for analyses of dependence of these characteristics on each other on stand and small-scale landscape level. Several studies recently were conducted in similar stands aross Europe and this simple fact provides good options for comparison of results and allows assuming of characteristics of some processes on general scale.

# 2 Aims of the thesis

The thesis is conducted to describe and better understand the structural features of mountain spruce forest on selected site in Tatra mountains in northern Slovakia. Study stands are considered as natural forest stands, also stated as old-growth-stands, with no human influence for several decades. Therefore, they provide insight to natural processes which can help practitionaires and desision makers with management of spruce stands. The main aims are:

- 1. Describe structural characteristics (live trees, deadwood, regeneration) of the natural spruce forest at plot, stand and landscape level.
- 2. Identify the correlation between biotic and physiographic characteristics.

Furthermore, we discuss the possible role of past disturbances on the current forest structure based on obtained results and literature review.

#### 3 Review

#### 3.1 Natural and old-growth forests

Primary, never-logged and by human activity directly unaffected, forests all over the world are continuously losing their already very reduced area. This general fact is much stronger when considering only temperate forests, especially in northern hemispere (Fraver et al. 2009; Silander 2001). Such stands are scattered over the region (Europe and North America as most studies were undergone there) usually in relatively small refugies (Fraver et al. 2009), often located in mountain regions. It is clearly an outcome of long and more or less continuous human activity, be it direct wood exploitation or for example shepherding, resulting in reducing and/or altering forest stands and their structure (Silander 2001). This leaves primary forests only in distant or for some other reason hardly accessible regions (Fraver et al. 2009). Such situation only deepens the threat to their diversity and/or variability. Larger unaffected areas - in terms of thousand hectares and more - that for whatever reason avoided harvest or other type of high impact management are even more rare (in temperate zone particularly). However, exactly those stands can provide most information about disturbance - and dynamics in general - histories of forests (Fraver et al. 2009).

These stands cover high variety of tree structures, including standing and down dead trees and snags. Also both vertical and horizontal structures are very complex, creating mosaic of stand development phases (Franklin et al. 2002). This complexity is a result of various effects of different scale, severity and origin disturbances. Except direct human activity of course which is a very specific category and logically should not be present in these types of stands. The different forest stand structures should cover all stand development stages (Franklin et al. 2002).

Another category - although the differences might not be always significant - for study of natural forest structure is concept of old-growth forest. Old-growth forest could have been logged or somehow managed in the past but for extended period (several decades or more) evolved without further human intervention (Bauhus et al. 2009; Wirth et al 2009). During this non-intervention period, the stands are creating defined structures that should appear in natural - never-managed - forest or similar to those. Among these there is a wide range of tree sizes and presence of trees that are likely to die just because of their high age (Bauhus et al. 2009; Mosseler et al. 2003). This

concept was defined by several authors with more or less differences (Spies 2004; Wirth et al. 2009) and different concepts might not consider the human disturbance history with no regards to how distant past that was - as an accceptable condition in some approaches. This is based on fact whether the old-growth definition in given study is considering recovery of the past managed/affected stand back to conditions resembling that of never-managed stand. Anyway, old-growth stands should provide much higher variability than logged stands even compared to those where some steps were taken in order to increase their value in terms of nature conservation, as these managed stands still limit the variety and volume of processes leading to old-growth features (Keeton 2006). It is important to note that regarding subalpine Norway spruce (*Picea abies*) forests, even the well preserved refugees were in most cases historically affected by wood exploitation and probably even more by grazing (Motta et al. 2002) which probably left some residual impact to recent days, however it might not be visible or usually at least not significant. According to Korpel' (1989), the time necessary for the stand to erase evident results of previous human intervention in mountain or boreal spruce stands is from several decades to about one hundred years - which is approximately the time it takes for the decay of all but the largest logs (Zielonka 2006) – but in many other forest types it usually takes much longer and the impact of human activity can be seen even long after the direct logging residuals are decomposed.

Disturbances - discrete events changing resource availability and disrupting ecosystem or community (Pickett & White 1985) that happen over short period of time but affect the system in a long term future (Turner 2010) - and their patterns on both spatial and time scale influence the stand in its structure, composition and even function (Fraver & White 2005; Turner 2010). Combination of these patterns as well as interactions between them are the basis for several widely accepted concepts such as shifting mosaic steady-state (Bormann & Likens 1979), disturbance patch dynamics (Pickett & White 1985) or landscape equilibrium (Turner et al. 1993). Disturbance can occur on a large scale - we can talk about stand replacing disturbance. To this category belong mostly large forest fires and windstorms. Yet under certain circumstances the category is not exactly limited to those. The above mentioned events can also cause less severe disturbance which does not affect the whole stand but a fair part of it, be it as a compact area or more often patterns creating variable distribution across the stand – this form of larger scale disturbances is lately reffered to as a moderate or intermediate

disturbance (Woods 2004). For the mosaic or patchy dynamics of the stand, the smaller scale ones are of higher importance, with the intermediate disturbance able to result in similar pattern. This sort of disturbances is caused by death of a single tree or rather small group of trees leading to creation of various sized gaps in the otherwise close canopy (McCarthy 2001). These fine-scale dynamics are commonly associated with decrease of soil moisture - or moisture changes in general (Aakala et al. 2011; Allen et al. 2010) or in some cases also by variability of population dynamics of spruce bark beetle (Ips typographus) (Aakala et al. 2011) or other pests depending on the type of the stand. It is the combination of disturbance peaks (high frequency and severity of events) and relatively undisturbed growth periods what creates the mosaic structure (Fraver & White 2005). It is additionally affected by relatively rare moderate-severity wind disturbances (Fraver et al. 2008) or possibly other event of similar extent. The response of the stand to future disturbance, mostly the mid to large-scale ones, is influenced by the disturbance history of the stand - presence of the structures created as a result of previous disturbances, often several decades ago (Veblen et al. 1994; Svoboda et al. 2012).

## 3.2 Stand structure

These stands cover high variety of tree structures, including standing and down dead trees and snags. Also both vertical and horizontal structures are very complex, creating mosaic of stand development phases (Franklin et al. 2002). This is in great contrast with homogenous structure of even-aged spruce stands in the age class forestry concept which is used in majority of production forests. These managed stands often do not provide good conditions for natural regeneration and are therefore more vulnerable and less stabile should some extreme situation occur. However, selection forests might often resemble some of the features of old-growth stands at least in terms of diameter distribution and the presence of regeneration. Although even this exception is probably applicable only on certain phase of natural stand development (Korpel' 1989). This complexity of natural stands is a result of various effects of different scale, severity and origin disturbances. Except direct human activity of course which is a very specific category and logically should not be present in these types of stands. The different forest stand structures should cover all stand development stages (Franklin et al. 2002).

Conditions of natural or old-growth forest in general consist of structural features often combined with ecological aspects of a given area and were over time defined for many different areas of temperate forests (Burrascano et al. 2013). However, much more research have been done in North America compared to some other regions creating some unbalance in resource availability for comparison (Franklin et al. 2002; Lindenmayer et al. 2000). However, the amount of research done in Europe is still rather high (Burrascano et al. 2013) mostly in last decade. These structural definitions show great variability through the range of areas for which they were created (Burrascano et al. 2013; Turner 2010; Wells et al. 1998) as different climatic conditions and species composition also correspond with different types of disturbances, tree longevity, tree ages representing given successional stage etc. (Burrascano et al. 2013; Franklin et al 1987). Significant differences between the stands in a global scale are mostly based on different species composition, geographic and climatic conditions. Only quadratic mean diameter shows significant dependence on age class of the stand (Burrascano et al. 2013) even thought it is still influenced by species composition. It is also suggested that evaluation of such stand should focus not only on the final structures (i.e. biological legacies) but also - and perhaps more importantly - on processes that lead to their creation and maintaining (Burrascano et al. 2013; Franklin et al. 2002; Lindenmayer et al. 2000).

On a more fine scale majority of European studies are describing or examining mixed forest stands, most commonly mountain beech-fir (*Fagus sylvatica, Abies alba*) forests (Nagel & Svoboda 2008; Šamonil et al. 2009). Relatively recent studies often suggest that dynamics of spruce stands are to various extent different (Nagel & Svoboda, 2008; Svoboda et al. 2012; Zielonka et al. 2010). Taken even further many studies that are actually focused on Norway Spruce stands are coming from Scandinavian region (Kuuluvainen et al. 1998; Fraver et al. 2008). These studies are unfortunately for several reasons hardly applicable (at least not to full extent) on central European situation. The main of these reasons is the different type of most important disturbances. While large-scale disturbances by fire are described as the most frequent or important scenario in Northern Europe (Wallenius et al. 2005), windstorms and spruce bark beetle (*Ips typographus*) outbreaks - of various severity - are considered the most important mid to large-scale disturbances in central European region (Janda et al. 2010; Panayotov et al. 2011; Svoboda et al. 2014; Wermelinger 2004). Until quite

recently wind and bark beetle disturbances, which often follow each other, were of low importance for research as these disturbances were considered to be of a minor and/or secondary role. Usually these types of events were considered a result of previous wrong management decisions (Svoboda et al. 2010). Relatively recent events of severe windstorms that caused serious damage on forest stands which was exploited by bark beetle, leading to large scale outbreaks, gave very good reason for reconsideration of this premise (Jonášová & Prach 2008; Panayotov et al. 2011; Svoboda et al. 2010; Svoboda et al. 2012) as these higher severity but low frequency disturbances are hard to detect in traditional methodology focusing on current or recent situation (Zielonka et al. 2010). Supporting results were obtained in sub-alpine Norway spruce forest in Tatra Mountains, Slovakia (Zielonka et al. 2010). Also in Western Carpathians, several rather large patches of more or less homogenous stands were observed and there is a reason to believe those can be a result of stand replacing, large-scale disturbance (Holeksa et al. 2007). Evidence of past stand replacing events was found also in natural forests in eastern part of Carpathian chain (Svoboda et al. 2014). Only good knowledge about disturbances and their regimes starting from the single tree death gap dynamics up to stand replacing high severity but low frequency disturbances can provide us with understanding the structural patterns and help us recognize and possibly model stand development, ultimately providing means to identify, predict and possibly avoid threats that might arise (Zielonka et al. 2010). These observations have to be conducted on multiple levels if the sought outcome is the understanding of disturbance regime range up to landscape level (Svoboda et al. 2014).

#### 3.3 Dead wood

Important for stand dynamics is the presence of coarse woody debris. Coarse woody debris is dead wood present in the stand in form of fallen logs and branches, eventually also parts of highly decomposed logs etc. (Harmon et al. 1986, Waddell 2002). In some older works, standing dead trees are also considered a part of coarse woody debris (Harmon et al. 1986) but lately the term usually refers to lying pieces only. Minimum diameter of the dead wood to be considered as a part of coarse woody debris is highly variable among studies, typically the minimum is between 7.5 and 15 cm (Harmon et al. 1986), lately 10 cm diameter minimum seems to be rather common. Dead wood of lower diameter is considered as fine woody debris in those studies that make difference between these two categories (Harmon et al. 1986). Importance of the

dead wood lies partially in the simple fact that its removal also means removal of resources for future generations but there are also biochemical processes that cause alteration to conditions on the dead wood substrate (Hendrickson 1991) which might be favourable for new regeneration. The decay process is usually modeled as constant rate althought it varies with age of the dead wood and size of its pieces (Zell et al. 2009; Zielonka 2006). During the process there is a number of microhabitats which are otherwise unavailable or very rare in given conditions. The volume of coarse woody debris present in the stand is also an important factor as higher volume means wider variablity of microhabitats and also more surface of the dead wood available at given time for any associated species (Müller & Bütler 2010). Average volume is much higher in old-growth or unmanaged stands than in managed ones as a result of timber extraction and dead wood removal in the latter. However, there are attempts to define and maintain certain levels of dead wood that should be present in any stand (Banas et al. 2014; Müller & Bütler 2010) in order to improve species diversity and stability of the stand. It is important to note that even if the volume of dead wood reaches rather high levels in some stands, the portion of ground it covers is small in comparison with the general area - generally not exceeding 10% (Zielonka 2006; Svoboda et al. 2010). Comparison of studies done in managed - which includes removal of dead wood and thinning - and in unmanaged stands hints that abundance of dead wood is a really important factor for future regeneration establishment (Svoboda et al. 2010).

#### 3.4 Regeneration

The pattern and density of regeneration in unmanaged forests are different in dependence on species composition and several biotic and abiotic/physiographic factors. However, some traits are common for wide variety of stand conditions and species. Among these one of high relevance is the presence and volume of dead wood (Harmon et al. 1986). Norway spruce (*Picea abies*) as a main target of this study has been proven to reflect the presence of CWD in the stand in conditions of temperate mountain forests (Zielonka 2006; Svoboda et al. 2010). Similar pattern was observed also in Scandinavian boreal forests of the same dominant specie (Hörnberg et al. 1995). The percentage of regeneration clustered on dead wood is rather high compared to relatively low portion of ground covered by it (Svoboda et al. 2010; Zielonka 2006). The reason of this pattern is seen as improved conditions on decaying logs. These logs provide higher variability of microhabitats and certain level of isolation of seedlings

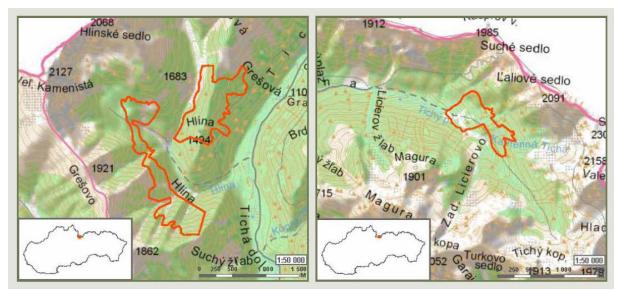
from the rest of the plants on the forest floor (Harmon & Franklin 1989) giving the newly established seedlings an advantage for the beginning of their growth especially in the stands where the structure was recently affected by death of portion of dominant trees providing good conditions for some other plants, namely ferns which can, under given circumstances, become major competitors and ultimately even suppress the spruce regeneration (Bače et al. 2009). This paired with the decomposition process results in the decreasing number of seedlings/saplings growing on dead wood with their increasing size (Holeksa et al. 2007; Svoboda et al. 2010; Zielonka 2006). Size in this context substitutes age - to some extent and in comparative way only. During the decay process some characteristics of the wood get altered in very profittable way for new seedlings. For example the water capacity is often higher than that of mineral soil (Zell et al. 2009; Zielonka 2006). Nitrogen content is increasing in the process, even though this increase is not as significant for conifers as observed in some broadleaf species (Hendrickson 1991). These conditions are also stimulating for some micorhizal fungi and their presence is further stimulating the growth of new regeneration (Zielonka 2006). As a result of this, regeneration in some stands reflects lines of formerly decayed logs and similar pattern can be often seen even among fully grown trees (Bače et al. 2009; Janda et al. 2010; Svoboda et al. 2010). The dead logs in the stand however provide not only suitable substrate for growth but on steep slopes also provide mechanical protection in several ways. The logs prevent or diminish the litter removal from the plot and they also to certain level block movement of stones and snow down the slope which protects especially young trees from bending or breakdown (Agee & Smith 1984; Holeksa 2001).

# 4 Materials and Methods

## 4.1 Site and plot selection

The study area is located in High Tatra mountains, northern Slovakia. The area is a part of Tatra National Park, founded in 1949. Since 1993 it is classified as biosphere reserve by UNESCO Man and the biosphere programme. Since 2004 the NP is also a part of Natura 2000 ecological network.

Six old-growth forest areas acknowledged in NPR (NNR) Tichá dolina (Tichá dolina, Hlinná dolina with 2 polygons, Žerucha and two old-growth forest residuals) cover 221 ha out of 5967 ha area of NPR (NNR) which was established in 1991 but the area was a part of strict reserve since 1959 (Jasík & Polák 2011).



**Fig. 1**. Polygons of old-growth spruce forests in which data were collected, Hlinná dolina on the left and Tichá dolina on the righ side. Maps published in Jasík & Polák (2011).

The study polygons were selected based on historical records, satellite images and previous observations as those were considered the most preserved in the region. Two polygons were selected in NPR (NNR) Tichá Dolina, polygons in Tichá and Hlinná Dolina. In each of the two valleys 16 plots were established. Study plots cover the elevation range from 1327 to 1507 m a.s.l. Average annual temperature in the area ranges between 2 and 2.5°C. Average annual total precipitation vary from 1200 to 1300 mm. The geological substrate consists mainly from deluvial granites. Soils consist of mosaic of brown forest soils and humus-rich forest soils. Both these are loamy soils with medium to high content of gravel and high supply of humus. Both types are wellaerated poor on accessible nutrients and exhibit moderately to highly acidic pH (Korpel' 1989).

A network of 2ha squares (141.2 x 141.2m) was established for individual plot selection. In each of these squares a lesser concentric square representing area of 0.5 ha was created in order to avoid potential overlapping of research plots. Three randomly generated points were chosen in each of smaller square which could be used as actual center of sample plot. Only if the point was at place unsuitable for research plot the second or subsequently third spot were used. As unsuitable were defined places like bedrock or extremely wet spots. If there appeared to be tracks of human activity evident stumps etc - the plot should have been deemed unacceptable too. Individual plot center points were found using GPS and marked with iron pin for future ability to locate the spot again. Each sample plot was given unique ID containg first three letters from the name of the valley (TIC for Tichá or HLI for Hlinná) followed by three digit number. These IDs are used in distinguishing plots in graphs and tables in results chapter. Established sample plots were circles of 0.1 ha area (radius 17.84 m). In case of rather young and very dense stand (with density of 1200 trees per ha or higher), smaller plots  $-500 \text{ m}^2$  (radius 12.62 m) - were optionally allowed. For all established plots, altitude of the center, slope and aspect of the slope were determined. The same general design was used in several recent studies in Norway spruce stands in temperate European zone (Trotsiuk et al. 2014; Svoboda et al. 2014).

# 4.2 Data collection

All data collection was conducted in August 2013.

#### 4.2.1 Trees

Each live or dead tree over 100 mm DBH was marked with associated number and measured using metric tape with diameter function. This is considered easier than two tangential measures that would be needed if caliper is used. For every tree a record of DBH and species was set. Further we recorded whether the tree is live or dead, in case of dead trees also a state of decay was noted according to five degree scale as follows:

 First degree shortly after tree death with residuals of smallest branches or even needles/leaves.

- Second class was assigned to trees with potential remnants of small branches but no residuals of needles/leaves.
- Third class trees already showed lack of serious portion of branches yet with the large branches still remaining.
- Fourth degree covers trees with only few largest branches remaining and often already showing a stem break.
- 5) Fifth class was given to snags of under 2 m of height in apparently advanced degree of decay.

Rough estimation of dead tree height was also noted in 10 m categories. Trees were also classified in two categories for trees creating the main canopy layer or lower layer. To the second category belong trees under 75% height of highest trees in the plot. Released and supressed trees were also distinguished, criteria for supressed trees were more than 50% of their crown growing in direct shading of surrounding trees, potentially also with additionally deformed crown shape. Microhabitat of each tree was also noted depending if it is growing in a pit, on a mound, dead wood residuals or general other substrate. The first two mentioned categories are results of a tree uprooting.

#### 4.2.2 Dead wood

For collecting data about lying dead wood Line intersect method was used (Harmon & Sexton 1996). This method was chosen because of its easy application during terrain work, relatively simple calculation and widespread use in similar studies. Star-shaped composition of transect lines was used. Starting in the middle of the sample plot, five 20 m long transect lines were going under the angle of 0°, 72°, 144°, 216° and 288° respectively giving us total lenght of intersections 100 m, which is considered minimum for accurate estimations. Total lenghts of under 100 m of transect lines, which were used in some usually older studies, were deemed inaccurate as a result of not enough representative sample (Harmon & Sexton 1996). As lying log or large branch was considered any piece of dead wood which created angle less than 45° with the ground. Only logs which had their axis still over the surface of surrounding terrain were measured. For every lying log with diameter over 100 mm, its diameter, species and decay class were recorded. Diameter was measured rounded to centimetres, and the measurment should be done tangentially to axis of the log, not to the transect line. Five

decay classes were used, defined according to visual condition and by the depth a knife could penetrate to the wood (Sippola & Renvall 1999):

- Recently dead tree with hard wood and still fresh phloem and almost intact bark. Knife does not go deeper than few milimetres.
- Wood still hard with mostly complete bark but phloem is not present anymore. Knife penetrates up to 20 mm into the wood.
- Wood starts to be decayed, large parts of bark are missing or at least loosened. Knife can go 30 to 50 mm deep.
- Most wood decayed and soft, most bark is missing sometimes even parts of the wood. whole blade penetrates easily into the wood.
- 5) Log is very soft and when attempted to lift it tends to break apart, often covered by mosses or lichens.

Diameter data were further used for estimation of volume of dead wood in the stand. Formula for estimating volume per unit area (Harmon & Sexton 1996; Van Wagner 1968; Warren & Olsen 1964) was used.

$$V = \pi^2 * \sum D^2 / 8 * L$$

Where:

- V is the estimated volume, in our case in m<sup>3</sup>\*ha<sup>-1</sup>.
- $\pi$  is constant, in some literature (Harmon & Sexton 1996) 9.869 is used instead of  $\pi^2$  but those are identical numbers.
- D is diameter of each individual log in cm.
- L is the total lenght of transect lines in each plot, 100 m in our case as five 20 m long transects were used.

The formula can also use diameter in metres giving the result in  $m^{3}$ \* $m^{-2}$  (Harmon & Sexton 1996) but since we were looking for volume per ha the first option is more suitable than the second one which would have to be further multiplied by ten thousand - conversion of  $m^{2}$  to ha. Even more since the diameters were measured in millimeters but rounded to centimeters because it is rather hard to measure dead logs of higher degrees of decay with milimeter accuracy.

The star-shape of transect lines used also prevents bias that can be caused by some prevalent direction of lying logs when paralel lines are used. This is of concern mostly in managed stands as a result of felling in certain direction but since we were working on slope the possibility of some deviation from normal or random distribution seems to be there too.

#### 4.2.3 Regeneration

For each plot, saplings were counted in three categories - 0.5 to 1.3 m; 1.3 to 2.5 m and 2.5 m and up, up to 100 mm diameter. Data about this size category, species and substrate/terrain were recorded for each sapling. Substrate/terrain categories were the same as for measured trees: pit, mound, dead wood and general other conditions. In case of high amount - especially of lowest size saplings, as these can be really numerous on certain plots - qualified estimation was recorded.

#### 4.3 Data processing

#### 4.3.1 Trees

For each of total of 32 plots, forming two groups (for Tichá and Hlinná dolina) of 16 plots each, the density of trees per ha was calculated, the same was done for the total from each group and for all data pooled together in order to see if there is any general change on a bit larger scale. The graph and table were created for Spruce and Rowan together. For view of amount of Rowan individuals per ha based on data of each plot and for percentaghe of Rowan in the stands, a second graph was created. For exact source numbers for this graph, data regarding different species are added to the table with general density of trees. Simple linear regression was used to verify possible significant correlation between density of trees and number of dead trees present. The possible relation of tree density to geographical elevation was also tested using linear regression on total pooled data and on datasets for each valley.

For each plot the percentage of Norway spruce and Rowan trees was calculated and set into a graph. Average density and corresponding percentage of Rowan trees was determined for each group of plots and for the total sum of plots.

Thinnest and thickest measured trees were found for each plot and and together with spread of DBH, these data formed table and a graph. In case the highest measured diameter in a given plot was referring to a snag, nearest value from a standing tree even potentially dead but still keeping its height and habitus was taken instead. The graph is better for overview of the situation while the table provides exact numbers/data. The table includes also mean DBH, standard deviation of DBH and median value. For each plot measured trees were assigned to 50 mm diameter range classes and a graph of their distribution among these classes was created. The diameter classes centered at 125 mm; 175 mm and so on in order to have all classes possibly present in its full range - if size classes were centered typically at 100 mm; 150 mm etc. we would have received biased data because half of the first class range would not have been present as result of minimal recorded diameter. Similar graphs were again created for both groups of plots and also for all plots together in order to see if there is some change on larger scales. In attempt to see if there are any patterns spread across the samples, the diameter distribution graphs for each single plot were sorted into three groups based on general commonalities of the curve shape. First category more or less reflect the ideal inverse Jshape, the second exhibits to some extent one peak with wide base which could be interpreted as roughly unimodal distribution and the last category covers variety of shapes where there is rather high number of trees constant or with multiple small peaks and drops over several size classes before the numbers rapidly diminish in the large classes. For the two valleys and for pooled data the graphs of diameter class distribution for live and dead trees comparison were done to show if the distribution is the same or not. Basal area was calculated from measured DBH values using standard formula BA =  $\pi$  \* (DBH/2)<sup>2</sup>. Value used for  $\pi$  is 3.14159. As all calculations are done in metric system units it was possible to use this simpliest form of equation with no need of any more complicated unit conversion (i.e. meters to inches or vice versa). Linear regressions were run for mean diameter and basal area of the individual plots testing their possible dependance on density of trees per ha on respective plots.

Additionally, for each plot the number of trees and also snags with diameter over 500 mm was set into a graph. Snag here refers to a remnant of under 2 m height (but over 1.3 m in order to record appropriate DBH), corresponding to class five of above mentioned classification of standing dead trees. This was done to reflect presence of large trees, possibly aproaching their physical age, in different plots. Percentage was

calculated for each category. Simple statistical test was done for both large trees and snags in relation to tree density, linear regression was used for this purpose.

Data regarding percentual contribution of suppressed live trees and lower canopy layer live trees were tested for relation between one another. Further the two datasets were tested for correlation with density of trees on sample plot, number of large trees present on a plot and elevation. Linear regression analysis was used for all the testing.

#### 4.3.2 Dead wood

Total estimated volume of CWD per ha was calculated and the data were used for a graph showing comparison between individual plots. For groups of plots and for all plots together average values for these larger samples were calculated. The value of volume of dead wood per ha for groups of plots in each valley is possibly giving the best view on the state of the stands in this matter. Since the study was done on relatively steep slopes which might result in sort of removal of dead wood from plots, simple linear regression was run to test this hypothesis based on assumption that should this removal effect exist it would be more intensive with increasing steepness, resulting in relatively lower volumes on such plots. The same method was used to test relation between dead wood volume and altitudinal gradient for pool of all data and for groups of plots representing each of the two valleys. Analysis was conducted for relation between density of standing trees (both for only living ones and for all including standing dead ones) and volume of CWD. Linear regression was used to identify possible connection between volume of coarse woody debris and regeneration of Norway spruce and Rowan again on the two different sample size levels.

#### 4.3.3 Regeneration

From regeneration data a graph of amount of saplings per ha of Spruce and Rowan in all size classes was created as a comparison of individual plots, groups of plots and total average. Similar graph was created for percentage of different species. For Spruce, graph comparing numbers of saplings in all classes in each plot in relation to substrate was created, the same graph was done for percentage of saplings present on given substrate. For both groups of plots and for total summary of plots another graph showing percentage of Spruce saplings on different substrates was created to visualize

possible preference of substrate for seedlings in larger samples. These additional graphs were not considered for Rowan as it is not the target specie. For separated Norway spruce and Rowan species regeneration linear regression examining amount of regeneration in dependence on density of trees and subsequently on combination of stand density and volume of dead wood present were done (both for total pool of data and for each valley). To test if there is a trend in preference of substrate among seedlings and saplings a  $x^2$  test was used. The analysis was used to test if the distribution of young individuals is the same for all possible substrates. Further analysis, again using linear regression was used to determine possible dependence of regeneration density on altitude.

# 5 Results

## 5.1 Plots

In each valley one of the established plots had only  $500 \text{ m}^2$  area. This is admittedly only a circumstance, ratio of bigger and smaller plots was not set in the design as size of the sample plot depends on the density of trees on site.

Plots in Tichá dolina were established in range of 1327 to 1497 m a.s.l., in Hlinná dolina the range was from 1368 to 1507 m a.s.l. according to GPS data. Steepnes of slope on the plots varied from 17° to 33.3° and 17.8° to 36° in Tichá and Hlinná respectively. Values for particular plots are sumarized in **Table 1**.

Plot ID	Area [m <sup>2</sup> ]	Slope [%]	Aspect [°]	Altitude [m a.s.l.]	Plot ID	Area [m <sup>2</sup> ]	Slope [%]	Aspect [°]	Altitude [m a.s.l.]
TIC_071	1000	19.3	352	1470	HLI_178	1000	36.0	280	1368
TIC_089	1000	35.0	354	1454	HLI_206	1000	17.8	192	1407
TIC_111	1000	29.8	232	1466	HLI_213	1000	30.6	138	1397
TIC_125	1000	22.5	24	1431	HLI_213_2	1000	26.2	272	1403
TIC_128	1000	27.0	3	1447	HLI_216	1000	32.0	298	1473
TIC_131	1000	26.0	10	1403	HLI_232	1000	18.1	158	1430
TIC_134	1000	19.5	74	1398	HLI_235	1000	21.7	164	1406
TIC_164	1000	20.0	38	1344	HLI_250	1000	32.5	290	1448
TIC_161	500	21.7	8	1399	HLI_256	1000	33.0	91	1418
TIC_167	1000	33.0	28	1327	HLI_268	1000	26.9	145	1484
TIC_185	1000	20.5	148	1369	HLI_271	1000	27.3	176	1481
TIC_068	1000	23.5	268	1440	HLI_274	1000	34.6	179	1456
TIC_102	1000	17.0	180	1383	HLI_283	1000	30.3	278	1467
TIC_105	1000	17.0	194	1427	HLI_289	500	32.0	92	1464
TIC_108	1000	33.3	202	1471	HLI_314	1000	32.6	278	1507
TIC_148	1000	29.0	208	1497	HLI_339	1000	30.8	96	1454

**Table 1.** Size and basic geomorphological parameters of individual sample plots.

#### 5.2 Trees

Observed density of trees per ha ranges from 280 to 1200 (280 to 1180 in Tichá dolina and 350 to 1200 in Hlinná). Total average density was calculated to 597 trees per ha, for groups of plots in the two valleys the averages are 632 and 561 trees per ha for Tichá and Hlinná respectively (**Fig. 2**). High amount of dead standing trees was observed, especially at some particular plots. The percentage of dead standing trees including snags is 26.8% in total, 19.6% for Tichá and 33.2% for Hlinná. This gives us

values of live tree density which is 437 trees per ha (508 per ha for Tichá and 375 per ha in Hlinná).

Plot ID	Live trees [N * ha <sup>-1</sup> ]	Dead trees [N * ha <sup>-1</sup> ]	All standing [N * ha⁻¹]	Sorbus trees [N * ha <sup>-1</sup> ]	Sorbus [%]
TIC_071	300	270	570	0	0.0
TIC_089	600	50	650	70	10.8
TIC_111	200	180	380	0	0.0
TIC_125	470	20	490	40	8.2
TIC_128	230	50	280	0	0.0
TIC_131	910	60	970	70	7.2
TIC_134	440	40	480	60	12.5
TIC_164	750	30	780	190	24.4
TIC_161	1180	0	1180	60	5.1
TIC_167	630	210	840	20	2.4
TIC_185	470	60	530	30	5.7
TIC_068	270	420	690	0	0.0
TIC_102	440	150	590	30	5.1
TIC_105	260	140	400	20	5.0
TIC_108	870	80	950	20	2.1
TIC_148	110	220	330	30	9.1
HLI_178	210	250	460	60	13
HLI_206	470	90	560	0	0.0
HLI_213	50	320	370	0	0.0
HLI_213_2	250	100	350	50	14.3
HLI_216	270	240	510	80	15.7
HLI_232	310	60	370	0	0.0
HLI_235	580	390	970	0	0.0
HLI_250	70	370	440	30	6.8
HLI_256	350	140	490	40	8.2
HLI_268	400	50	450	0	0.0
HLI_271	440	200	640	0	0.0
HLI_274	340	80	420	0	0.0
HLI_283	540	70	610	110	18.0
HLI_289	360	840	1200	140	11.7
HLI_314	430	90	520	140	27.0
HLI_339	510	110	620	30	4.8
Average Tichá	508	124	632	40	6.3
Average Hlinná	375	186	561	43	7.6
Total mean	437	160	597	41	6.9

**Table 2**. Density of live, dead and all standing trees per ha on individual plots. Density and percentage of Sorbus trees, again per ha.

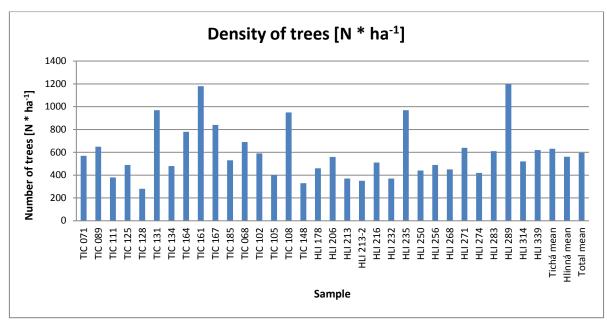
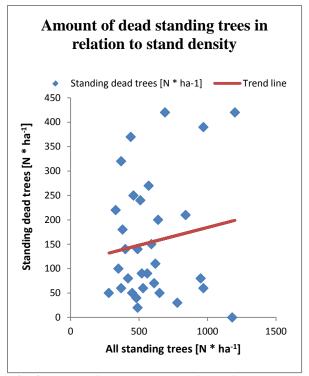
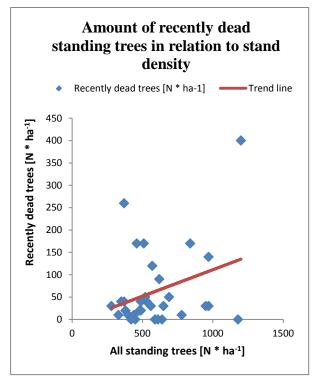


Fig. 2. Density of all standing trees on individual plots, in each valley and total dataset.

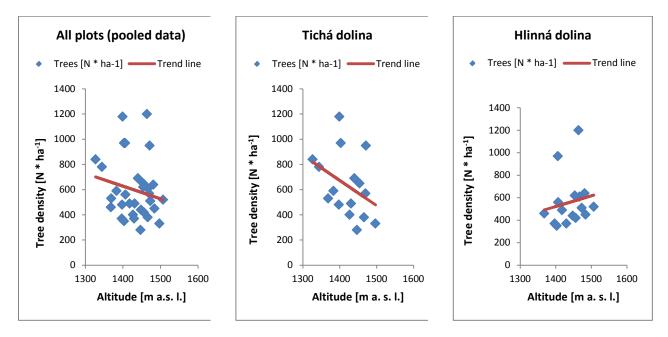
Linear regression shows no significant correlation between number of dead trees and density of all standing trees (P-value = 0.44) (**Fig. 3**). A bit lower but still insignificant P-value was obtained by running linear regression for recently dead trees only (P-value = 0.074) (**Fig. 4**). No significance was proven for relation of tree density to altitudinal gradient across total pool of data (P-value = 0.31) though the regression curve indicates slight negative relation to increasing elevation. On level of single valleys, no significance was proven either (P-value = 0.147 for Tichá and 0.55 for Hlinná). The decrease can be seen on regression curve for Tichá, in Hlinná quite contrary slight increase in density along the gradient can be observed (**Fig. 5**).



**Fig. 3**. No significant relation was found for density of dead standing trees and total density of the stand, the trend is visible though (P-value = 0.44).



**Fig. 4**. For recently dead standing trees only no relation to stand density was proven, trend can be seen (P-value = 0.074).



#### Density of trees in relation to altitude

**Fig. 5.** Relation of tree density to elevation for all data (first chart) and individual valleys (second and third chart). None of the relations were proven statistically significant.

As partialy seen in the **Table 2** number of Rowan trees (with DBH over 100 mm), as admixture species, per ha ranges from none to 190, the percentage ranges from 0 to 24.4%. Average density for Tichá is 40 trees per ha which equals to 6.3%, for Hlinná the density is 43 Rowan trees per ha representing 7.6%. Total average density is 41 Rowan trees per ha, total average percentage of Rowan trees is 6.9% (**Fig. 6**). No relation was found between density of stand and portion of Sorbus trees present.

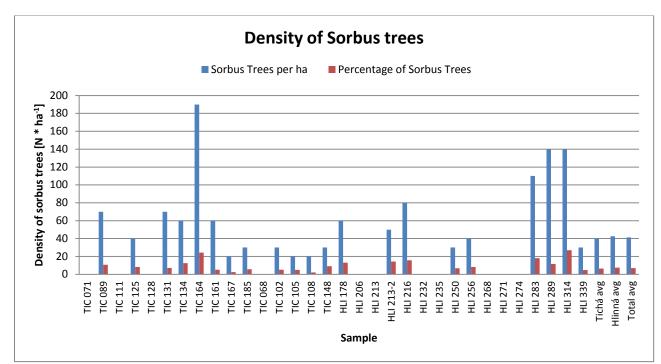


Fig. 6. Number of Rowan (sorbus) trees per ha and their percentual contribution to the stand.

Measured tree diameters are covering relatively wide range of 823 mm (705 and 823 mm for Tichá and Hlinná respectively), with the thinnest tree being 100 mm diameter (minimum accounted DBH) and the largest one 923 mm. Total mean diameter is 314 mm, for Tichá dolina 331 mm and for Hlinná dolina 296 mm. Mean diameter in single plots is shown in **Fig. 7**. Mean DBH values and also values of standard deviation and median of DBH in individual plots, each valley and in total are summarized in **Table 3**. The spread of diameters along with thinnest and thickest tree diameter measured in given sample can be seen also in **Fig. 8**. Linear regression shows strong negative correlation between increasing density of trees and mean diameter (P-value < 0.001) and allows us to explain up to 73% of variation of mean diameter just by the tree density on the individual plots (**Fig. 10**). The same results also with P-values under 0.001 were proven for data of each of the two valleys, suggesting this relation is visible starting from relatively low area levels.

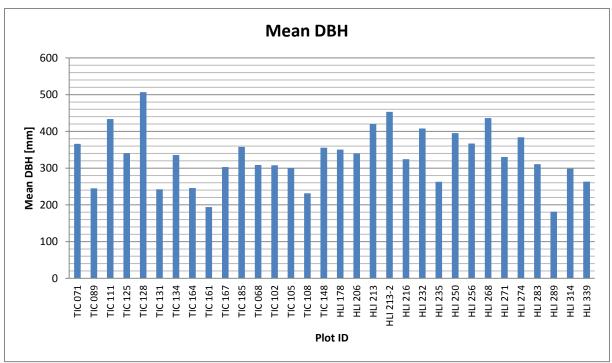


Fig. 7. Mean DBH on individual sample plots.

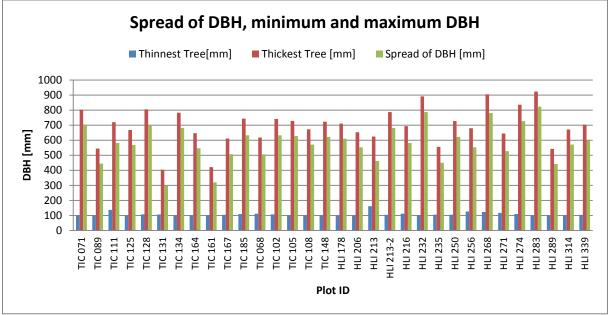
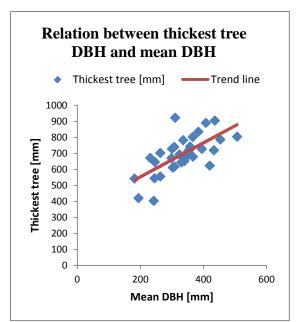


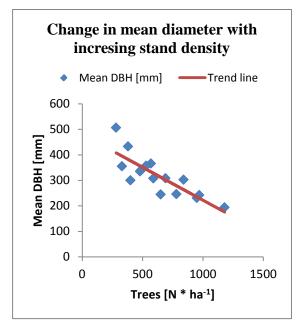
Fig. 8. Minimal and maximal values of DBH and range of DBH on each individual sample plot.

Plot ID	Mean DBH [mm]	Standard deviation	Median of DBH [mm]	Minimum DBH [mm]	Maximum DBH [mm]	DBH range [mm]
TIC_071	366	157.1	382	100	803	703
TIC_089	245	107.8	217	100	545	445
TIC_111	433	147.6	445	138	720	582
TIC_125	341	143.6	318	100	668	568
TIC_128	507	209.2	530	108	805	697
 TIC_131	242	99.8	222	107	404	297
 TIC_134	336	150.5	321	101	783	682
TIC_164	246	137.4	189	100	647	547
TIC_161	194	65.8	190	101	421	320
TIC_167	303	122.0	303	105	612	507
TIC_185	358	181.0	349	110	743	633
TIC_068	309	123.6	296	112	618	506
TIC_102	308	178.3	268	108	741	633
TIC_105	300	197.8	212	100	729	629
TIC_108	231	138.9	187	101	672	571
TIC_148	356	174.3	329	101	723	622
HLI_178	351	174.0	363	100	711	611
HLI_206	340	179.9	300	100	653	553
HLI_213	420	151.0	415	162	624	462
HLI_213_2	453	190.8	511	105	787	682
HLI_216	324	139.3	306	112	694	582
HLI_232	408	168.8	410	104	891	787
HLI_235	263	101.3	259	106	556	450
HLI_250	395	149.5	407	106	728	622
HLI_256	367	162.6	328	127	680	553
HLI_268	436	161.8	393	124	905	781
HLI_271	330	147.2	324	117	645	528
HLI_274	384	201.7	360	110	836	726
HLI_283	311	180.3	252	100	923	823
HLI_289	181	94.6	152	100	543	443
HLI_314	299	158.3	268	100	671	571
HLI_339	263	166.0	170	105	703	598
Tichá	298	158.2	262	100	805	705
Hlinná	331	171.1	304	100	923	823
Total	314	165.2	279	100	923	823

**Table 3**. Mean, median and standard deviation of DBH. Minimal and maximal values and range of DBH for individual plots and larger samples.

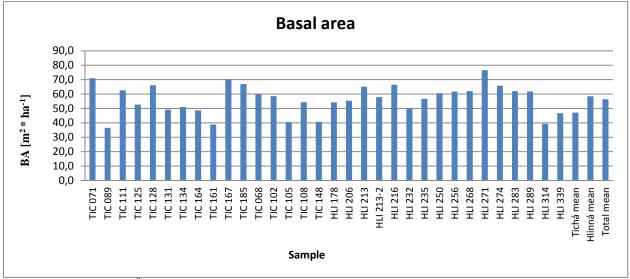


**Fig. 9**. Relation between thickest tree on the plot and mean DBH on the respective plot shows clear correlation (P-value <. 0.001, linear regression was used).

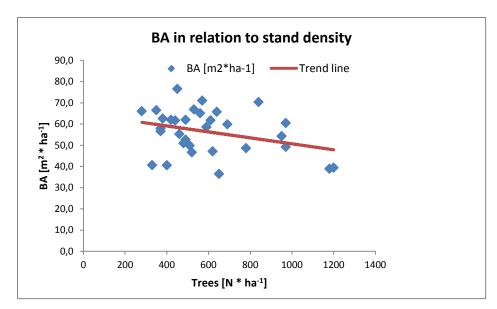


**Fig. 10**. Mean diameter was proven to be significantly (P-value < 0.001) decreasing with increasing density of the stand.

Calculated basal area per ha is presented in **Fig. 11**. Total mean basal area is 56.3  $m^{2}$ \*ha<sup>-1</sup>(54.3  $m^{2}$ \*ha<sup>-1</sup> and 58.4  $m^{2}$ \*ha<sup>-1</sup> for Tichá and Hlinná). Minimal observed basal area is 36.5  $m^{2}$ \*ha<sup>-1</sup>while maximum is 76.6  $m^{2}$ \*ha<sup>-1</sup>. Linear regression used for basal area per ha in dependance on density of trees proved there is no significant relation on 5% confidence level (P-value = 0.07; 0.48 and 0.07 for Tichá and Hlinná when examined independently) (**Fig. 12**).



**Fig. 11.** Basal area in m<sup>3</sup> per ha for each individual plot and means for larger samples.



**Fig. 12.** BA shows slight decreasing trend with increasing stand density this trend was not proven significant however (P-value = 0.07).

There was on average 77 trees over 500 mm DBH per ha which equals to 12.9% (67 and 87 per ha in Tichá and Hlinná, representing 10.6% and 15.5% respectively). Mean number of snags, also of 500 mm DBH and more, was 9 per ha in total (1.5%), with the same amount also for both groups of plots (corresponding to 1.4% in Tichá and 1.6% in Hlinná). More detailed view of large trees and snags per ha in individual plots can be seen in **Fig. 13**. While the presence of large trees shows significant negative dependence on the density of trees (P-value < 0.001, for independently examined groups of plots from Tichá and Hlinná both P-values are less than 0.01), no reliable relation was found for large snags in this matter (P-value = 0.87) (**Fig. 14**).

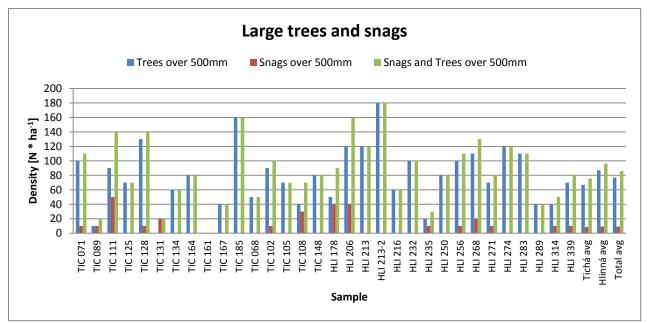
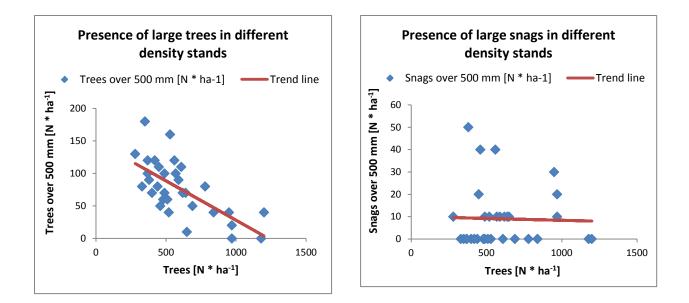
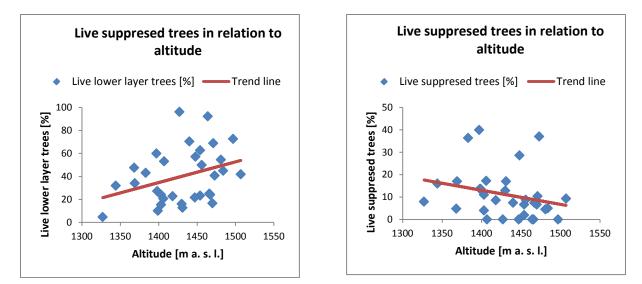


Fig. 13. The density of large trees and snags per ha in each sample plot and average values for larger datasets.



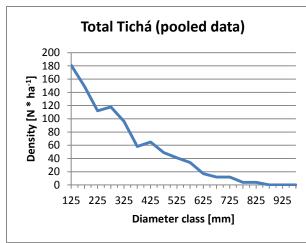
**Fig. 14.** Amount of large trees significantly negatively correlate with increase in stand density (P-value < 0.001). For presence of large snags (defined as dead standing residuals over 1.3 m but lower than 2 m) no significance was proven and even no apparent trend is visible.

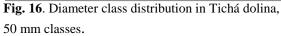
The percentage of live suppressed trees present on the plots ranges from 0 to 37%, 11.1% on average (0 to 36.4% in Tichá and 0 to 37% in Hlinná, averages 10.2% and 11.9% respectively). The contribution of lower canopy layer live trees to total density goes from 4.8% to 96.2%, average 40.2% (for Tichá the full extent of the range, for Hlinná 16.1 to 92.3%, averages 35.9% and 44.6%). All relations of portion of suppressed or lower canopy layer trees to density of the stand, number of large trees present and between the two groups proved to be largely insignificant. The dependence on altitude was not proven significant either but regression curves for both categories show evident trend (P-value = 0.15 for suppressed and 0.059 for lower layer trees). This trend is increasing with elevation for lower layer trees and decreasing for presence of suppressed trees in higher altitude (**Fig. 15**).

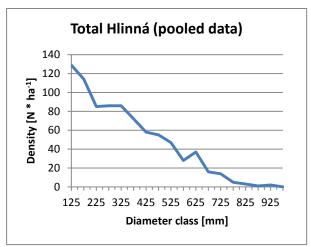


**Fig. 15.** Portion of suppressed and lower canopy layer trees show insignificant (P-values = 0.15 and 0.059 respectively) but apparent trends in relation to altitude.

Diameter classes distribution in each valley and throughout all samples can be seen in **Fig. 16 - 18**. Distributions in each sample plot are available in the appendix (**Fig. 36 – 41**). Results are very variable among the plots but some basic commonalities can be seen, this is subjective interpretation however. With increasing sample size - on a level of the whole valley or even complete dataset - the shape of diameter class curve is evidently getting closer to the shape of inverse J-shape although it is again a subjective point of view. The distribution of different diameter class curve patterns among the plots was generally even with the diverse group of curves showing multiple peaks and drops being slightly more common than other two categories (12 plots compared to 10 in each of the other groups). Except for the constant/multiple peaks category, the number of plots in each category seriously differ between the two valleys (**Table 4**). Plots included in multiple peaks category are more or less randomly scattered across the polygons. The plots with diameter distribution curve resembling unimodal distribution are also partially randomly distributed but some plots seem to be forming small groups (more apparent in Hlinná Dolina). All the plots with diameter distribution curve reflecting inverse J-shape in both valleys are forming clusters (**Fig. 19**).







**Fig 17**. Diameter class distribution in Hlinná dolina, 50 mm classes.



Fig 18. Diameter class distribution across the whole dataset, 50 mm classes.

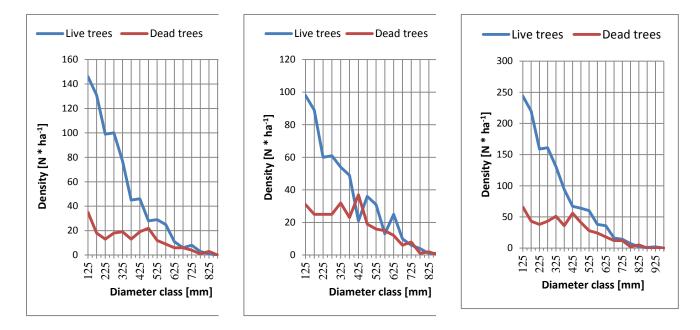
**Table 4.** Frequency of different shapes of diameter distribution curve among individual sample plots. The names of categories are generally simplified shapes which are resembled by the actual curve.

	Multiple peaks/drops	Inverse J-shape	Unimodal
Tichá dolina	6	7	3
Hlinná dolina	6	3	7
Total	12	10	10



**Fig. 19.** Positions of plots in the polygons with respect to the shape of their diameter distribution curve. Multiple peaks/drops shown as red dots, inverse J-shape as blue dots and unimodal distribution as green dots. Map layer taken from <a href="http://www.arcgis.com/home/webmap/viewer.html?webmap=b1baa822ed614b3184fab3ecb2deb8e5">http://www.arcgis.com/home/webmap/viewer.html?webmap=b1baa822ed614b3184fab3ecb2deb8e5</a> 9<sup>th</sup> March 2015.

The comparison graphs of diameter class distribution among live and dead trees (**Fig. 20**) show that live trees in all cases more or less reflect the inverse J-shape curve, while the density of dead trees is almost constant up to slightly over 400 mm diameter where a peak occurs and then the desity is rapidly deacreasing. Large dead trees are rather rare, usually in the form of snags as defined in methodics. The peak is best visible in pooled data for Hlinná dolina where it is also followed by sudden drop in live trees density which results in dead trees being more numerous in given size class than live trees.



#### Diameter distribution of live and dead standing trees

**Fig. 20**. Diameter distribution of live and dead trees in Tichá dolina (first chart), Hlinná dolina (second chart) and throughout the whole dataset (third chart).

#### 5.3 Dead wood

Estimated volume of CWD ranges from  $24 \text{ m}^3 \text{*ha}^{-1}$  to  $308 \text{ m}^3 \text{*ha}^{-1}$  with average of  $120 \text{ m}^3 \text{*ha}^{-1}$  through all samples. Minimum of  $24 \text{ m}^3 \text{*ha}^{-1}$  and maximum of  $308 \text{ m}^3 \text{*ha}^{-1}$  were obtained in Tichá which has average of  $125 \text{ m}^3 \text{*ha}^{-1}$ . For Hlinná minimum was  $11.97 \text{ m}^3 \text{*ha}^{-1}$  and maximum  $214 \text{ m}^3 \text{*ha}^{-1}$ , average volume there was  $115 \text{ m}^3 \text{*ha}^{-1}$ . Volumes of CWD estimated for individual plots can be seen in **Fig. 21**. No significant relation between steepness of slope and volume of CWD was found (P-value = 0.068). In fact the regression curve indicates that the volume of dead wood gets slightly higher with increasing steepness of the slope (**Fig. 22**). No relation was found between density of standing trees over 100 mm DBH (for only living ones as well as for all including dead standing trees) and volume of CWD (**Fig. 23**). No significance was found also for change of dead wood volume along the altitudinal gradient (P-value = 0.12). The regression curve however reveals very slight increase in volume in higher elevations. When regression was run on level of individual valleys the significance of increase of CWD along elevation gradient was proven for Tichá (P-value = 0.027) but not for Hlinná (P-value = 0.4) for which there seems to be slight opposite trend (**Fig. 24**).

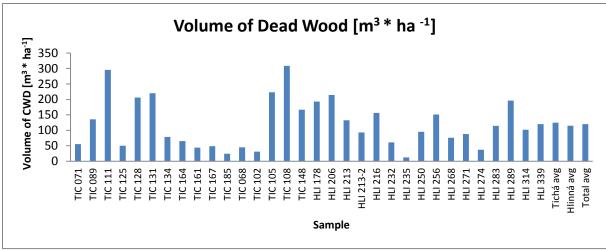
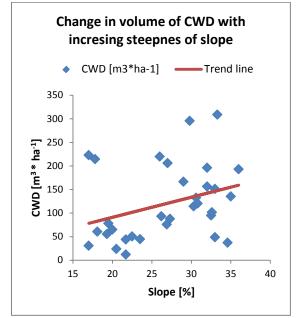
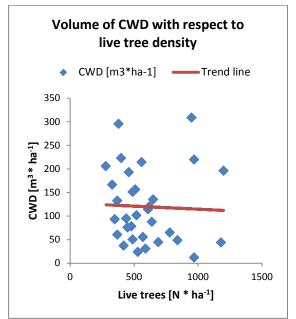


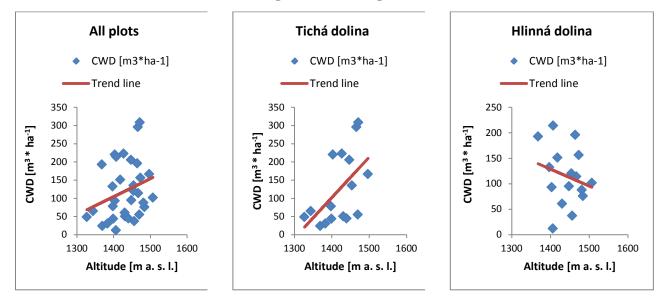
Fig. 21. Volume of CWD on individual plots and average values for both valleys and total pool of data.



**Fig. 22.** Opposite to theory that there would be less CWD on steeper slopes the trend seems to be increasing with increasing steepness. No significance was proven however (P-value = 0.068).



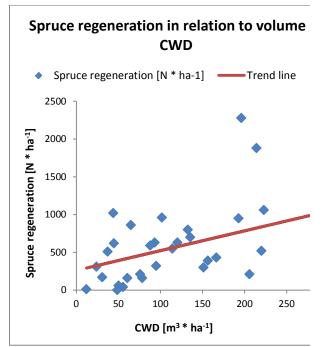
**Fig. 23**. No relation was proven between live tree density and volume of CWD (P-value = 0.83).



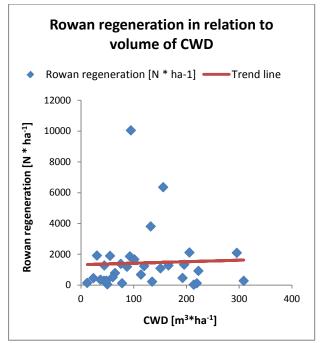
# **CWD** along altitudinal gradient

**Fig. 24.** Pooled data from all plots indicate increasing trend of increase in volume of CWD along altitudinal gradient, this trend was not significant (P-value = 0.12). For data from Tichá only the trend is even significant (P-value = 0.027). Contrary data from Hlinná show insignificant (P-value = 0.4) slight opposite trend.

Although only about 16% of variability in amount of Norway spruce regeneration can be explained by it, the linear regression shows that it is significantly influenced by volume of coarse woody debris present in the stand (P-value = 0.022) (**Fig. 25**). Significant for Hlinná (P-value = 0.001), insignificant (P-value = 0.33) but the same trend indicating for Tichá. The same test proved no reliable connection between volume of dead wood present and regeneration of Rowan at any scale (P-value = 0.83 for all data and 0.56 and 0.87 for Tichá and Hlinná individually) (**Fig. 26**).



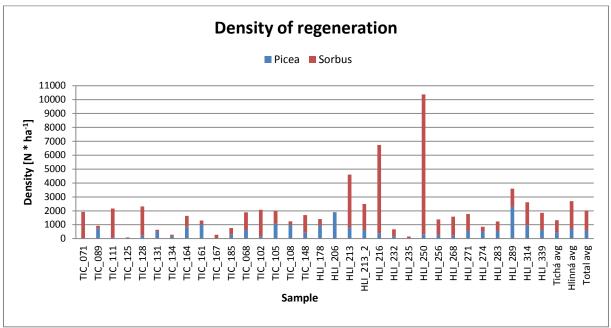
**Fig. 25**. The amount of Norway spruce (*Picea abies*) is significantly (P-value = 0.022) increasing with increase in volume of CWD.



**Fig. 26.** No relation was proven for amount of Rowan (*Sorbus*) regeneration and volume of CWD present (P-value = 0.83).

## 5.4 Regeneration

Average number of saplings and young trees up to 100 mm DBH is 2015 per ha, 575 for Norway spruce and 1440 for Rowan, showing high variability across the plots. For individual plots volume of regenaration of different species **Fig. 27** was created. Rowan saplings are more numerous however mostly in the smallest size class (88% individuals under 1.3 m and only 1% in the 2.5 m and up category) (**Fig. 28**).



**Fig. 27**. The amount of regeneration of Norway spruce (Picea) and Rowan (Sorbus) on each plot, average values calculated for larger samples.

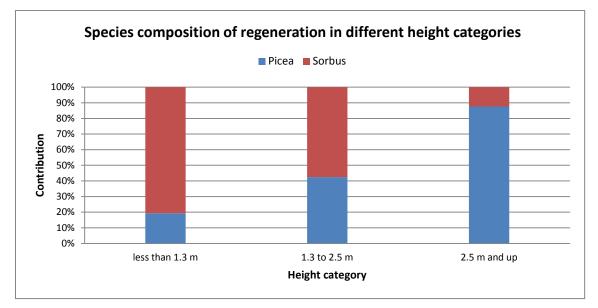
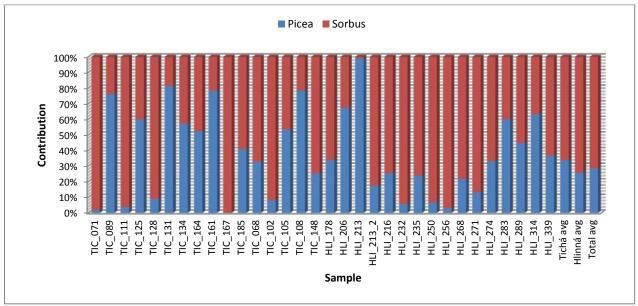


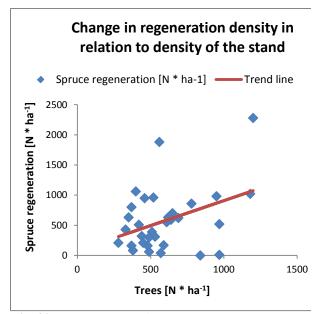
Fig. 28. Species composition of regeneration in each recorded height class (pooled data from all plots).

## Species composition of regeneration

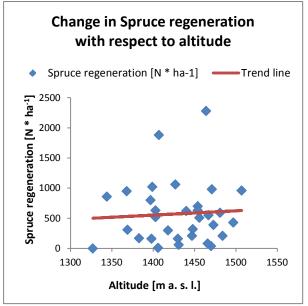


**Fig. 29**. Percentual contribution of Spruce (*Picea*) and Rowan (*Sorbus*) to total amount of regeneration on scale starting from individual plot up to pool of all collected data.

Relative composition of regeneration by Spruce and Rowan is highly variable across the plots with average Spruce contribution of 28.5% (Fig. 29). Regression analysis shows that there is higher regeneration recruitment of Norway spruce in more dense stands (P-value = 0.028) (Fig. 30). The same correlation is insignificant in both valleys when tested individually (P-values = 0.066 and 0.076 for Tichá and Hlinná respectively), the trends are still apparent however. Even higher was proven the importance of density of the stand in combination with abundance of coarse woody debris. Increase in both of these independent variables can explain up to 33% of variability in amount of young individuals present. P-value in this case is 0.003 (Insignificant for Tichá with rather strong trend, P-value = 0.07, and clearly significant for Hlinná P-value < 0.001). Neither of the same analyses resulted in significant relation of Rowan regeneration density on tested factors (for density P-value = 0.11 for combination of density and CWD volume P-value = 0.29). Only for Tichá individually there is apparent and even significant trend of decreasing amount of regeneration with increasing density of stand (P-value = 0.03). Even there is no significance of the relation when CWD volume is added as second independent variable, though. No significance was proven for relation of regeneration density to altitude (P-value = 0.74), regression curve indicates very slight increase along the gradient (Fig. 31).

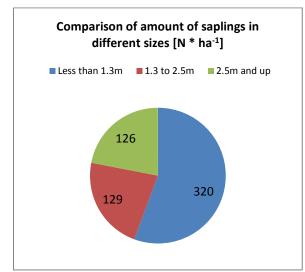


**Fig. 30.** Spruce regeneration was proven to increase in more dense stands (P-value = 0.028).

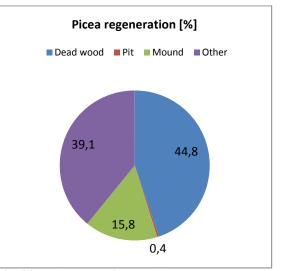


**Fig. 31.** No relation was found between Spruce regeneration density and altitude. (P-value = 0.74)

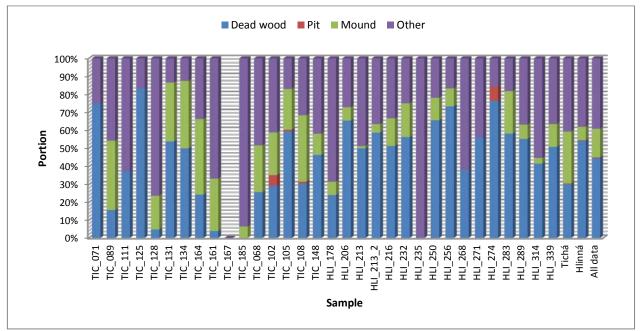
Majority of Norway spruce regeneration (55.6%) belong to the lowest hight class (0.5 to 1.3m), while second and third classes contains similar amount of trees (22.4% and 22.0% respectively) (**Fig. 32**). With no regards to size class of the regeneration, most young Norway spruce individuals was found on dead wood (44.8%), 39.1% was found on general other substrate without no exact classification, 15.8% was growing on mounds and only 0.4% was found in pits (**Fig. 33**). Finer scale data for individual plots and groups for each valley regarding percentage and actual numbers of young individuals per ha are presented in **Fig. 34** and **Fig. 35** respectively.



**Fig. 32**. Distribution of Norway spruce regeneration in different size classes.

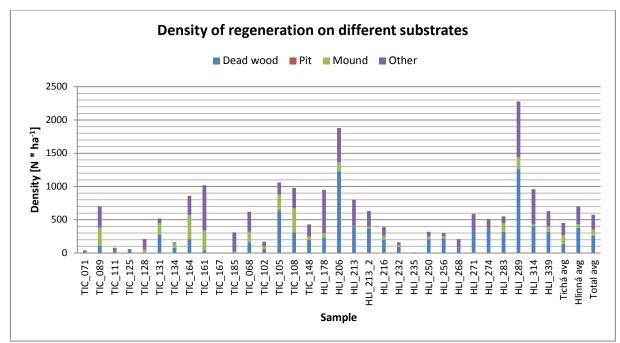


**Fig. 33**. Substrate preferences in Norway spruce regeneration with no respect to size classes.



# **Regeneration on different substrates**

**Fig. 34**. Percentage of Norway spruce regeneration on different substrates on finer scale. Larger samples are added for comparison.



**Fig. 35.** Substrate preferences in Norway spruce regeneration as amount of individuals per ha for individual plots, for larger samples average values are presented.

Statistically the distribution is manifesting great deviation from random distribution (P-value < 0.001) and therefore reveals apparent substrate preferences. Especially in the smallest size class (under 1.3), there is apparent overabundance of new individuals growing on dead wood while quite contrary, in largest size class (2.5m up to 100 mm DBH) overwhelming majority of saplings is growing on non-specific substrate (classified as other). P-values under 0.001 and the same general pattern were obtained as results also for each valley.

# 6 Discussion

## 6.1 Plots

The occurence of  $500m^2$  plots is in methodics defined by density of trees over 1200 per ha while actual plots of this size have density of 1180 and exactly 1200 trees per ha. This is a result of slight overestimation of visual assessment of stand conditions on site. Though the deviation does not seem so high to cause a real bias in the data considering the data were multiplied also for the larger (0.1 ha) plots in order to get values coresponding to 1ha. Furthermore, there was exactly one smaller plot in each valley anyway. In general, the data cover rather wide spectrum of geomorphological conditions in terms of altitude (139 m range), steepness of slope (19 % range, starting at 17 %) and exposition (samples oriented more or less in all direction in Tichá and all except nothern oriented slopes in Hlinná) which should allow for diverse enough data to avoid generalization of data typical for rather specific abiotic conditions. Although none of examined plots or even potential area which were further considered before actual plot was established provided any evidence of relatively recent human activity (stumps after felling etc.) some such remnants were spotted during movement across the area. The occurence of this evidence is of hardly imaginable reason considering some of them were seen in hardly accessible locations, on steep slopes. Of course some of these can be explained as activity done in order to maintain safety or quality of tracks in the area, some others however were on locations rather distant from any trail. On some potential sites Norway spruce trees were forming polycormones which are considered as clear result of previous intensive grazing which was historically affecting large part of the region. Such sites were not used for sample plots with no regards to the fact the trees were fully grown and indicating the pasturing events ended several decades ago at least.

#### 6.2 Trees

#### 6.2.1 Stand parameters

The variability of tree density among the plots leads to conclusion that the stands in examined area are subject of various small to mid-scale disturbance events. Results of some such might be seen right at the time the data collection was done. As evidence of this could be considered very high percentage of dead trees, sometimes recently dead or dying, present on some plots - usually result of bark beetle infestation. This was not however the case of many other plots no matter that we operated in not that big area -

all old-growth forest remnats in the reserve together, and we have not examined all of them, cover 221 ha (Jasík & Polák 2011). This observation is consistent with result of some recent studies that proved no significant relation of similarity of disturbance histories with decreasing distance between the stands (Trotsiuk et al 2014). The wide range of diameters on most of plots makes it hard to think about the plots being a subject of large, stand replacing, disturbance for extensive time period. Those events, caused usually by windstorms subsequently followed by large bark beetle outbreaks, are anyway present in the region (Zielonka et al. 2010). Frequency of these is low, they should be still considered as a factor of high importance however.

The average density of trees 437 live trees per ha (597 including recently dead trees) seems to be in line with other observations in similar conditions in temperate Europe (Panayotov et al. 2011; Svoboda et al. 2010; Trotsiuk et al. 2014). Some of these studies show higher density of live trees but accompanied by lower average basal area which can quite well explain the difference. Wide range of the density also seems to follow the same pattern, the values of extremes seem to reflect results from similar studies as well. Similarly, values of basal area and mean diameters more or less fit the pattern of other studies in mountain Norway spruce forests. The high percentage of dead trees as well as patchiness of their distribution also support the results obtained in similar study in Bulgaria (Panayotov et al. 2011). Since I was unable to statistically prove any dependence of number of recently dead trees and the density of the stand I would assume that the presence of standing dead trees is most likely result of random small to mid-scale events like bark beetle infestation or perhaps also death because of reaching the tree's physiological age, though there are no means to prove the latter and large dead standing trees are rare. Rowan trees appearing in very diverse densities rarely exceeding 10% of stand density and never being by far the largest trees on the plot give the impression of opprotunistic admixture species in the stands clearly dominated by Norway spruce.

No significant variation was found for basal area in relation to density of trees which may suggest that stands in the area are rather stable in volume throughout their development considering the density decreases with increasing mean diameter (up to 73% variabiliy explained by this dependence). The P-value was only slightly off so the chances that the correlation exists and could be proven possibly in a larger sample should not be neglected. In support of this speaks the fact that in Hlinná the P-value was

close to breaching the significance line while in Tichá only the regression curve slightly reflects such pattern but is no way close to being significant.

The presence of large trees in most plots and their relatively high average abundance (12.9%) again supports the concept of no stand replacing disturbance taking effect here over several decades at least. Furthermore the increasing numbers of large trees in negative relation to density of trees on a sample plot (the significance is higher on landscape level than it is on single valley level) while this relation is non-existent for snags of similar sizes favors the idea of randomly occuring small gap dynamics. The average percentage of large snags in each valley is the same which might even suggest that through different events the development of stands is reaching analogous structures. As large tree or snag respectively were considered individuals of 500 mm DBH and higher. This threshold was chosen as it is the nearest rounded value over the middle of the measured DBH range (biggest tree DBH is 923mm).

#### 6.2.2 Physiographic factors

The density of trees in general seems to be slightly decreasing with increasing elevation although no significance was proven and on lower level, for individual valleys this trend seems to be present in one of them while in the other it is virtually non-existent and even very slightly oriented in opposite direction. That leads to conclusion that the effect of elevation in this matter is either effective only on large scale area or wider span of altitudes or the altitude is not the only (main) factor behind this trend. Korpel' (1995) presents concept that density of spruce trees should increase with elevation but only until it reaches some optimal value in both and then decreases again towards the upper spruce tree line (which is by Korpel' (1989) set to zone 1400 – 1600 m a.s.l), data for Slovakia region only. It is very well possible the data were collected around the inflex point causing this variability of results.

The insignificant but evident decrease of amount of suppressed trees in higher elevation could be result of possible higher light demands for spruce trees with increasing altitude (Pisek & Winkler 1959). The opposite trend in percentage of lower layer trees present with increasing elevation might be a result of slightly higher vulnerability of main canopy level trees in higher elevation - closer to the ridge (Kulakowski & Veblen 2002).

#### 6.2.3 Disturbances

The high percentage of lower canopy layer trees while the presence of suppressed trees is much lower in respective plots fits the pattern described as old-growth structure or structure of stand recovering of rather severe but not completely stand replacing disturbance by Camp & Oliver (2004) or in sense of Korpel' (1989) fits the definition of late decay phase or successive regeneration phase of stand development which is in the same study suggested to be present for large portion of time in mountain spruce stands. No significant and mostly not even by regression curve indicated relations to other plot conditions lead to conclusion it is a general structure of the stand on large scale. Considering the extremely high range of variability this is probably a result of random, different events. Overally these results are again in line with the concept of mixed severity and scale disturbances (Panayotov et al. 2011; Trotsiuk et al. 2014; Woods 2004).

The diameter class distribution across the individual plots shows very variable patterns starting from those clearly reflecting ideal inverse J-shape, to weird curves with multiple peaks and drops. On larger sample, for data pooled for all plots of appropriate valley and even more for data pooled from all plots together, the distribution is increasingly better reflecting the inverse J-shape of the diameter class curve although the shape is far from ideal. This result suggests that the stands in general are evolving naturally with no recent really large scale disturbance event. These higher level samples are important as disturbance regimes - and the distribution curve is a result of these should be always conducted with respect to area of observation (Trotsiuk et al. 2014). Quite contrary, the increasing variability of the curve with more fine scale gives good base for assumption of importance of mid-severity disturbances - large enough to significantly influence 0.1 ha plot but not even close to affecting the whole stand or area. The frequency of diameter class distribution shape of individual plots is almost equal for all three categories throughout the whole sample, except for the slight increase in the category exhibiting multiple peaks and drops. It is much more variable however when the results for the two valleys are compared. The multiple peak/drop scenario which might point to regular small disturbance or mid-scale but lower severity ones is even at this level evenly distributed. The inverse J-shape curve – after generalization of course as there are usually some minor peaks or drops -is much more frequent (about two times) in Tichá dolina while quite the opposite results are found for the – again very

generalized - unimodal (single peak) distribution which is twice as often in Hlinná dolina. The inverse J-shape should apply for stands which are subject mainly to small, often single tree death, gap dynamics thus the result suggest the stands in Tichá are less affected by larger disturbances recently. Plots with this diameter distribution are even creating two groups/clusters which even further support this theory. This shape of diameter distribution curve should correspond with "selection phase" in sense of Korpel' (1989) which should be present in spruce stands in High Tatras most of the time (Korpel' 1989). Unimodal distribution on the other hand is usually a result of natural or human-induced high severity event of larger scale occurring in the past (Svoboda & Pouska 2008). The high amount of plots that reflect such distribution in Hlinná dolina gives the impression of rather large scale and higher severity events playing important role there in the formation of forest structures, supported also by the clustering (to some extent) of plots with diameter distribution curve resembling unimodal distribution. This can be possibly just a result of different severity of large-scale events affected by topography (Woods 2004). In general the results support the concept that neither solely small gap dynamics nor only the large scale, low frequency and high severity disturbances are shaping the old-growth stands. The structures hint that it is actually the combination of both including wide range of frequencies and magnitudes in between them. The resulting structures are outcome of mixture of events different in severity, frequency and influenced area (Panayotov et al. 2011; Trotsiuk et al. 2014; Woods 2004). This sort of regime is referred to as moderate disturbances. These can be represented by rather large area affecting disturbance with relatively lower frequency and severity or by event affecting many small areas across larger region with different severity (Trotsiuk et al. 2014; Woods 2004). The latter can be even caused by several agents therefore in the older concepts it would not be defined as one disturbance but rather a complex of small ones. These results and assumed reason of these facts follow results recently commonly observed in mountain spruce stands in Europe (Panayotov et al. 2011; Trotsiuk et al. 2014; Svoboda et al. 2014) including the variability at different sample levels (Trotsiuk et al. 2014).

The comparison of plots for size class distribution of live and dead trees follow the similar pattern as general results but the peak in density of dead trees in diameter class just over 400 mm which is present in all three graphs and especially visible in data from Hlinná dolina where it is even accompanied by sudden decrease of live trees of

this diameter suggests some sort of disturbance event of probably larger scale and severity. From this data however it is hard to distinguish if it is a result of historical event which created sort of generation gap or if it was caused by event, likely bark beetle infestation, which affected some relatively homogenous stand of mostly this diameter class. Taking into account that the dead trees are still present the latter option seems far more likely. At any rate the data show evidence of most trees dying in relatively smaller size while large dead trees are rare and even then mostly in form of a snag. This could be considered as result of fact that once the tree is released and has the opportunity to grow it has high chance of survival because most of the dying individuals are suppressed trees or trees growing in dense stand and therefore high competition, resulting in suboptimal light or nutrient availability conditions. Smaller trees are also more susceptible to collateral damage following death and fall of a large tree. These results in part follow the pattern observed in some other studies (Svoboda & Pouska 2008; Svoboda et al. 2010) where the dead trees are on average smaller than live ones. On the other hand, in the mentioned studies the general distribution of trees in both categories was unimodal with one universal peak which does not apply for this data. This unimodal distribution can be understood as development after major canopy release which migh have been caused either naturally or by human activity (Svoboda & Pouska 2008). This statement again supports the assumption the examined old-growth stands in Tichá and Hlinná dolina were not subject to high severity, possibly stand replacing disturbance, for rather long time period.

#### 6.3 Dead wood

Applied method for dead wood volume estimation using Line intersect method is very efficient in the way of easy and relatively fast data assessment on site and not complicated calculation after that. However, it has two major downsides. One of them is possible bias caused by some prevalent pattern in log orientation though this one can be easily overcome using non-paralel transect lines, in the manner this study did or similar (Waddell 2002). The second disadvantage, actually not necessarily of an issue, is the fact that the estimation works solely with diameters and thus is not providing data (unless additionally collected) for land cover calculation and alike functions. Estimated average volume of 120 m<sup>3</sup>\*ha<sup>-1</sup> exceeds fairly the dead wood volumes from Pol'ana biosphere reserve presented by Holeksa et al. (2007) as one of the highest volumes measured or estimated for mountain spruce-dominated forests in the whole Carpathian

chain, similar values were obtained in Bulgaria (Panayotov et al. 2011). The methodics there admittedly involved more parameters directly measured which seem to lead to more accurate calculation. On the other hand, measured logs minimum diameter in that study was 70 mm while we were starting at 100 mm. The difference is anyway rather high to be believed to occur only as a diverse methodics error. Other studies however present still much higher values (Janda et al. 2010; Korpel' 1989). Here it should be noted that the first mentioned study has taken place in slightly lower elevation and have pooled data from lower amount of different samples and the other one is not really up to date which might and might not have impact on the values we are comparing here. In general there are studies that present higher, often much higher volumes of dead wood but these are extreme values or values achieved on a limited number of plots (e.g. study from Beskid mountains, Jankovský (2004) - observed value of 170  $m^3$  per ha with the actual mean only slightly under 90  $\text{m}^3$  per ha and also in this case the study was performed in slightly lower elevation and on less steep slopes). Considering spruce forests in Carpathian chain are in general exhibiting higher dead wood volumes than alike stands in Alps (Holeksa et al. 2007; Motta et al. 2006) the volumes estimated in our stands pose as high for a given stand in terms of species and geomorphology. This also confirms the assumption that the stands were not affected by timber or dead wood removal for extensive time period. This condition is one of the criteria to define (secondary) old-growth forest and also for plot selection for this study. Contrary to a theory that on steep slopes some removal effect for dead logs may apply, no relation of steepnes of slope was proven. In the above mentioned study from Pol'ana reserve (Holeksa et al. 2007) some slight and insignificant decrease was spotted for dead wood along altitudinal gradient. Our data also show this relation to be insignificant but the regression curve indicates slight increase in volume with increasing altitude (for solely the data from Tichá this relation seems to be significant). This contradiction hints that perhaps the variability is actually random or there is another factor involved - aspect of the slope for example – this theory is supported by the fact the results vary between the valleys. Or of course it might require bigger sample size. Overally the high volume of dead wood is corresponding to the concept of important and characteristical presence of dead wood in different decay classes in mature pristine and old-growth forests (Harmon et al. 1986; Motta et al. 2006). The fallen dead wood was result of either windthrow or bark beetle infestation (or combination of both) as expected for this area. No residuals

of charcoal were spotted confirming that fire is not important disturbance agent in this region.

#### 6.4 Regeneration

As suggested in previous studies (Svoboda et al. 2010; Zielonka 2006) presence of dead wood in the stand is important factor for Norway spruce regeneration and our results clearly support this hypothesis. According to results of linear regression there is usually more seedlings and saplings on the plots with higher abundance of CWD (Pvalue = 0.022) this should not be a result of simple higher regeneration on some plots in general as no such evidence was proven for Rowan which had a lot of young individuals present in many plots (P-value = 0.83). Here it is however important to note that volume of dead wood is probably a driving factor only in combination with some other parameter (most likely the density of stand which also significantly positively influence the regeneration of Norway spruce on large scale, the trend is apparent already in individual valleys analyses) considering the significance was found only for one of the two valleys when examined on the lower scale level. Or there is still the simpliest explanation about not large enough sample sizes on this lower scale level. The mean amount of young individuals is low. This can be partially a matter of methodics as only individuals over 500 mm height were recorded, considering the decrease of density in higher size classes this could well cause the relatively low values in comparison with other studies (Holeksa et al. 2007; Svoboda et al. 2010; Zielonka 2006). The amount of regeneration is higher than results obtained in nearby stand in 1976 (Korpel' 1989, 487 individuals per ha, starting from 200 mm height) and even those were accepted as high enough to provide good base for natural regeneration. The decrease in density of regeneration with increasing size of individuals is clearly visible from the data with big decrease between 0.5 to 1.3 m category and the next one and rather low decrease between the two higher size categories. This pattern again confirms the results of several previous studies (Holeksa et al. 2007; Svoboda et al. 2010; Zielonka 2006). The great prevalence of Rowan seedlings in the smallest size category and their serious diminishing in larger categories is apparently a result of fast and numerous regeneration in early stages but only few can find suitable enough conditions to successfully fight the competition in long term. Some studies suggest that the density of regeneration of Norway spruce should vary along altitudinal gradient, these studies however disagree on the fact if the density should be decreasing (Pisek & Winkler 1959) as a result of

higher light demands in higher elevations or increasing as observed in Pol'ana biosphere reserve (Holeksa 2007). Our data have proven no significant relation of these parameters, regression curve is very slightly indicating increase along the gradient but it still seems that the altitudinal gradient has very little effect or it would take very wide elevation range for it to become of real importance. Perhaps the altitude matters in combination with some other specific factor which would to some extent explain the contradictory results of different studies. One such factor might be the general density of trees which is slightly and insignificantly decreasing with the increasing altitude. This affects the amount of light available and therefore the effect of altitudinal gradient is influencing the amount of regeneration indirectly in established stand. No significance was found for this combination of factors though.

As in several previous studies (Motta et al. 2006; Svoboda et al. 2010; Zielonka 2006) the importance of dead wood as a substrate for natural regeneration is visible from these results. Across all size classes of the regeneration the overabundance on dead wood is clearly evident and significant, especially for the smaller sizes while for larger saplings most individuals are growing on mineral soil. Here it is important to note that the density for larger saplings is about one third of the density of smaller ones which might slightly affect the data. However more important seems the idea of nurse log being already decomposed to the state we were unable to detect it. Considering there are studies suggesting higher percentage of regeneration is taking place on logs in high decay classes (Zielonka 2006) - although there are young individuals growing on relatively recently dead logs as well - and the time for the log to decay completely (Holeksa 2001; Holeksa et al. 2008; Zell et al. 2009), it seems to be possible explanation for this specious change of preferences in different size classes. According to Holeksa et al. (2008) the decay period increases greatly with increase in diameter of the log. Thus it is possible to assume that smaller logs, that are a bit more common than really large ones (not in volume but in numbers) and therefore providing more opportunities, have just already disappeared causing at least part of this imbalance. Other authors (Bače et al. 2009; Zielonka 2006) link the decrease of larger individuals on the logs to the higher competition on logs in higher decay classes. Of course another option could be the different rate of mortality on various substrates or perhaps combination of both. Possible bias in the analysis might be caused by the suboptimal data for  $\chi^2$  test. The reliability of  $\chi^2$  test is said to be decreasing when some of the

expected values are less than 5 which is the case considering very few individuals growing in the pits. Even though the P-values are so low that they would most likely prove significant even if they were few grades higher this fact is still worth a mention.

# 7 Conclusion

Forest structure across the examined plots shows fair amount of variability with several basic commonalities. Among those are unevenaged structure, presence of lower canopy layer and suppressed trees and wide span of DBH of trees suggesting continuous regeneration. The abundance of dead wood and evidently with it related natural regeneration indicate no noteworthy human intervention over long time period. That being said the forests fullfill the definition of old-growth forest in most of its versions. When compared with studies examining exact disturbance data in similar stands the data imply that neither purely small (single tree death) nor only large-scale, high severity (stand replacing) disturbances form these stands. Furthermore, most of the results follow the recently often spelled theory of the mixture of different severity and magnitude disturbances being the main driving factor in natural forest development. The individual stands are according to this comparison subject of small, occasionally mid-scale and severity - intermediate (these are suggested by certain degree of clustering of plots with similar diameter distribution curves) - events which results in very variable structure both inside the plots or stands and between them even when they are not too distant, spatial-wise.

Most results (observed data and analysis outcomes) are in line with the results or patterns observed in similar studies in mountain Norway spruce stands in central or eastern Europe, which supports both presence of general patterns and probably proper conduct of this thesis.

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# Appendix

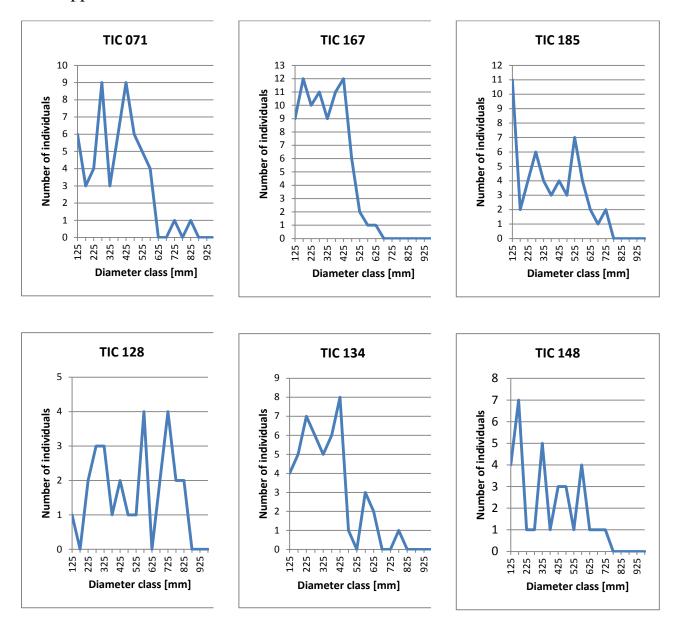


Fig. 36. Plots in Tichá dolina with diameter distribution curve considered as multiple peaks and drops.

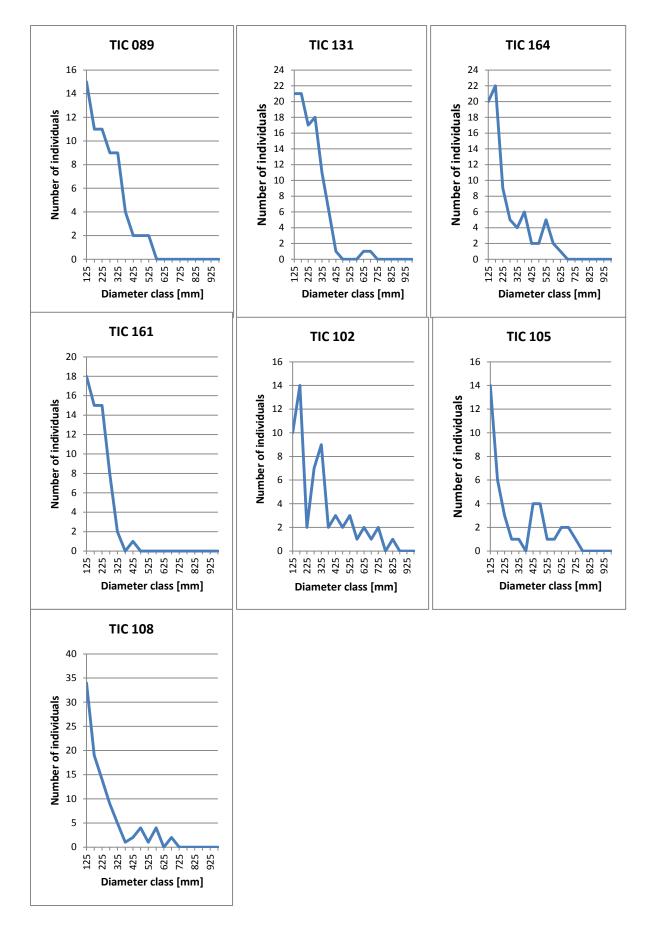


Fig. 37. Plots in Tichá dolina with diameter distribution curve resembling inverse-J shape.

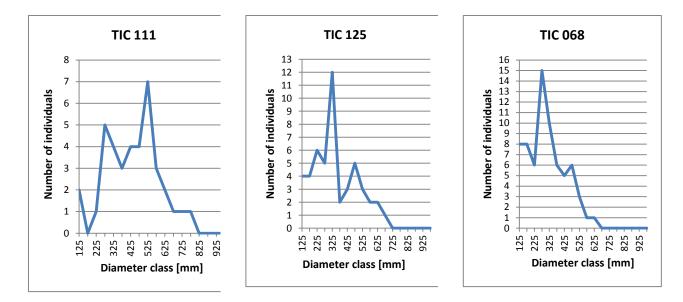


Fig 38. Plots in Tichá dolina with diameter distribution curve resembling unimodal distribution.

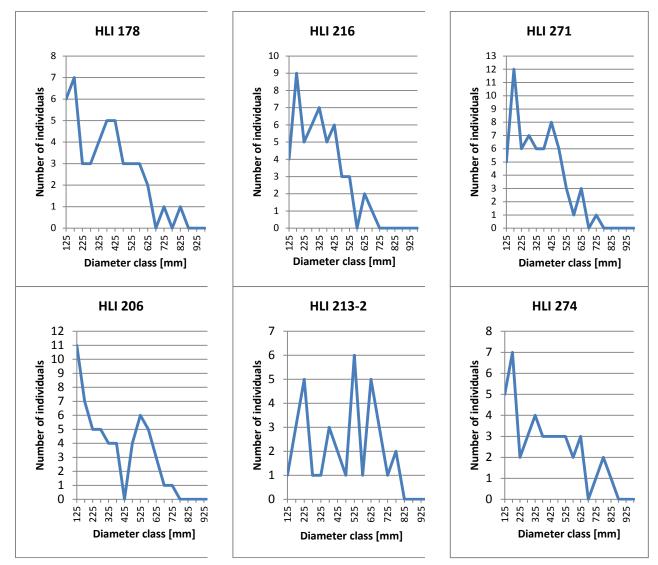


Fig 39. Plots in Hlinná dolina showing multiple peaks and drops in their diameter distribution curve.

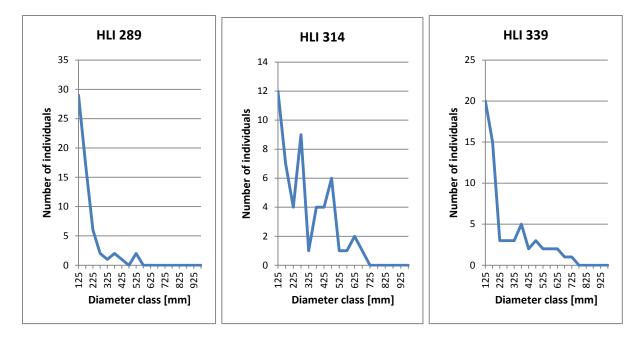
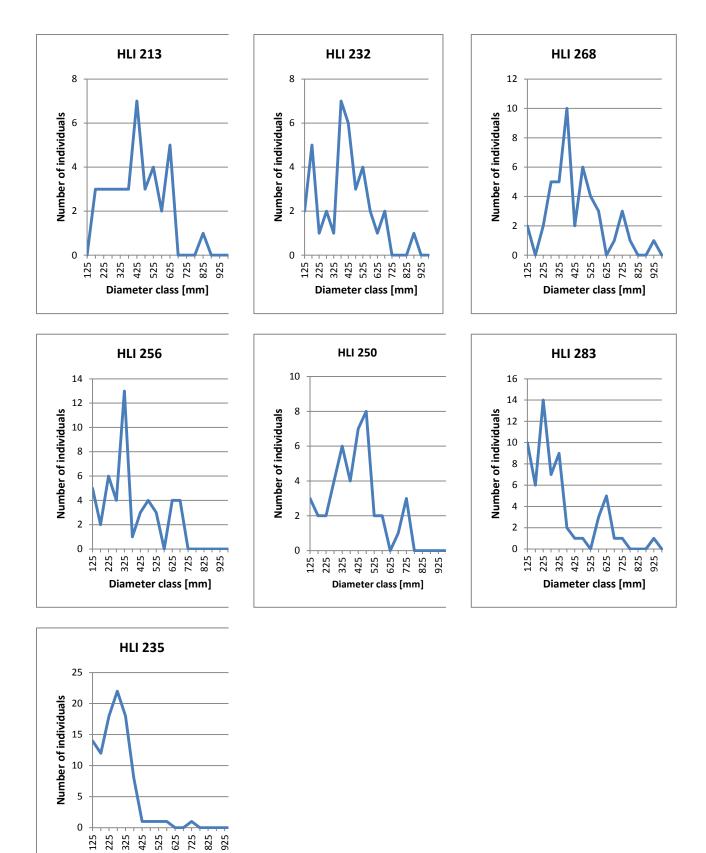


Fig. 40. Plots in Hlinná dolina reflecting inverse J-shape of diameter distribution curve.



**Fig. 41.** Plots in Hlinná dolina with diameter distribution curves interpreted as unimodal (resembling unimodal distribution).

Diameter class [mm]