CZECH UNIVERSITY OF LIFE SCIENCES PRAGUE

Faculty of Forestry and Wood Sciences

Department of Forest Ecology

Growth and mortality of natural regeneration shortly after dieback of tree layer of mountain spruce forest

DIPLOMA THESIS

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Thesis title

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Objectives of thesis

The aim of the study is to test the following hypothesis:
(1) The annual increment and mortality of individuals are independent of tree species
(2) The annual increment and mortality of individuals are independent of microsite
(3) The annual mortality of individuals decreases with the height of individual
(4) The annual increment is increasing with the height of individual
(5) Mortality of individuals is caused by intraspecific competition

Methodology

(1) The data collection focused on mortality and increment of permanently tagged individuals of regeneration on permanent research plots in the Sumava NP

(2) Mathematical and statistical processing of data

(3) Preparation of the thesis

The proposed extent of the thesis

50 pages

Keywords

Norway spruce, Picea abies, rowan, seedlings, mortality, microsite, increment

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Recommended information sources

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The Diploma Thesis Supervisor

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Prague on 10. 04. 2015

Declaration:

I hereby declare that I wrote this thesis by myself under the supervision of Ing. Radek Bače, Ph.D. I used literature and internet links that I noted in the list of references.

In Prague, April 17, 2015 Martin Havlíček

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Abstract:

This thesis describes the natural regeneration of mountain spruce forest in the Šumava National Park (Czech Republic) 7 years after a disturbance caused by windstorm and following bark beetle outbreak. Aim of this thesis was to analyze the height increment and mortality of natural regeneration in relation to different tree species, different microsite and also in relation to different height of individual. Another aim was to analyze whether the individuals of *Picea abies* intraspecific compete. The research was held on 10 plots with a net of square units 0.5 m x 0.5 m where all individuals of regeneration were marked, measured and evaluated. Height increment of Norway spruce was increasing with the height of individual. Height of rowan was decreasing with the higher height of individual due to browsing. The influence of microsite was crucial in relation to height increment, but it was marginal in relation to mortality. Dead wood was the best microsite for spruce height increment and it showed the lowest mortality. Mosses were the worst microsite for spruce height increment and it showed high mortality. Litter was a quite good microsite for height increment but mortality was here higher than by dead wood. Microsite influenced by vegetation showed high increment and also high mortality. The importance of intraspecific competition of *Picea abies* was not recorded as significant in this phase of regeneration.

Keywords: Norway spruce, Picea abies, rowan, seedlings, mortality, microsite, increment

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1. INTRODUCTION

The perception of nature is changing throughout the entire human evolution. The strong connection between human-hunter or human-gatherer with nature has modified into a strong connection between human-cultivator and nature. Human-cultivator has lived with the natural processes and tried to use them for his own benefit. This gradually led to a very strong influence of appearance of countryside in the human inhabited territory. In Central Europe, this change of countryside affected mainly forests, which used to cover almost all of the area (Kaplan et al. 2009). The conditions and lifestyle of recent past have been changing the human perception of the land. Due to the increasing demand of today's society for natural appearance of the countryside and for the natural processes, the perception of the land as having only an agricultural potential has weakened. Establishing of natural protected areas began and a nature-close management as a coherent act leading to more natural appearance of the countryside developed.

One field of the scientific interest, considering the natural processes, is the natural regeneration of mountain spruce forests, which is the topic of this thesis. The Šumava Natural Park provides a suitable area for research of this process. In the past a different approaches of management influenced the forest stands in Šumava Mountains and the relicts of the primeval forest can also be found here (Průša 1990). The forest management in this national park was in the time of writing of this thesis a very hot public topic. New Act about Šumava National Park was proposed, consequently rejected and some contradictory opinions on the natural processes in Šumava National Park were presented to the public. This thesis describes the natural regeneration of mountain spruce forest in the most valuable areas of the Šumava National Park, 7 years after a disturbance caused by windstorm Kyrill followed by the bark beetle outbreak. This thesis should lead to a better understanding of the mountain spruce forest dynamics in conditions of the Central Europe.

2. AIMS

The aim of this study was to test following hypothesis:

(1) The annual increment and mortality of individuals are independent of tree species

(2) The annual increment and mortality of individuals are independent of microsite

(3) The annual mortality of individuals decreases with the height of individual

(4) The annual height increment is increasing with the height of individual

(5) Mortality of individuals is caused by intraspecific competition

3. LITERATURE REVIEW

3.1. Mountain spruce forest

Mountain spruce forests create a supramontane vegetation cover of many Central European mountains. The dominant tree species is Norway spruce (*Picea abies*) and the admixed tree species is mostly only rowan (*Sorbus aucuparia*). Very rarely also sycamore maple (*Acer pseudoplatanus*), Eupean silver fir (*Abies alba*) or European beech (*Fagus sylvatica*) occur. Such an appearance is similar to the forests of North-western Europe. The natural mountain spruce forests in Šumava mountains occur on the highest positions of top mountain ridges (1200 m. above sea level and more) or in the severe climatic conditions of Šumava plains (Křenová 2008, Čada et al. 2013). The original virgin forests perished approximately till the year 1900 with some exceptions like Trojmezná forest or few other hardly accessible sites of mountain flanks. Despite the original virgin forests have been almost destroyed, there are forests in part of the Šumava National Park where natural processes of selection and adaptation create a new generation of Central European mountain spruce forests, which are developing without any direct human influence (Křenová 2008).

3.1.1. Spruce virgin forest

It is not easy to asses, what is an original Norway spruce virgin forest, and what is it not, because there are only very few fragments of such a forest left and due to this fact the evaluation is difficult. Some specialists claim that there are no untouched zonal spruce forests in the Central Europe, which could serve for the dynamics and structure inference of such forests. According to Míchal (not published) a true spruce virgin forests look quite exotic. They are usually very sparse, and they have vividly feathered trees and due to the presence of light gaps without any secured saplings, they seem to be in a permanent decay. The share of dead standing trees in the main tree layer is commonly more than 15 %.

Despite that the stand does not die across the board. A spruce virgin forest is overfilled by decaying wood. This fact can be explained due to the strong dieback of living stock (every year 0.9 – 2.5 %), while the process of decay in the cold climate can last up to 150 years. The amount of saplings under 130 cm does not reach more than 1 500 individuals per hectare and usually the rowan prevails (Svoboda 2005).

A true evaluation of the status and origin of a forest stand is difficult and requires an extensive filed survey. Some scientists (Franklin et al. 1981) use a simple method of evaluation. They call a forest of primeval origin such a stand, which has following three structural signs:

1) There are massive (in sense of thick) trees. The thickness of trees correlates with the age of trees and so they can be evaluate as old trees.

2) There are massive standing dead trees. The dieback of old trees is a natural part of natural forest dynamics and the presence of such trees proves the ongoing natural processes.

3) The last sign are the decaying logs in different stage of decay.

The presence of massive living trees, massive dead trees and decaying wood refers about the fact that the human activities probably did not influence the forest very much. Such an evaluation fits also to some parts of the Trojmezná forest in Šuamva National Park (Svoboda 2005).

3.2. Disturbances

A disturbance is classified as a transition event, which is disrupting or it causes mortality of one individual as well as many individuals. As a result of a disturbance a new place and possibility of new generation of the same species or another species arises. Disturbances are one of the main driving forces of forest dynamics and variability. Disturbances are caused due to natural influence or due to the human activity. Natural disturbances contribute to the countryside diversity, to the species diversity and to the ecosystem diversity. Ecosystems are not static. They are adapted to restore after a natural disturbance, which is a required part of the system

(Kulakowski & Bebi 2004). Forest stands differ in their sensibility to disturbances. This depends on the local conditions and on the stand characteristics. That's why after a disturbing event a mosaic of disrupted, partly disrupted and not disrupted stands is developed. This mosaic of different structure and composition plays a role in the stand resistance to next coming disturbances (Kulakowski & Bebi 2004).

Large scale disrupting leads to individual ecosystems restoration and it creates the growth characteristics. The species structure and composition are crucial in further development of the stands after the disturbance (Franklin et al. 2002). The disturbances cause the canopy opening and they play an important role in the creation and arrangement of the communities.

The soil disturbances are important for the forest dynamics. They support the germination and also the specie richness (Mayer et al. 2004). During large scale disturbances caused by bark and wood boring insect the soil disintegration does not appear. For that reason, the forest regeneration is more difficult and the dependence on the regeneration bank is more significant.

Till recent time the influence of disturbances on the forest dynamics in the Central Europe was marginalized. The reason for this may be the small area cover of natural forest, where the effect of disturbances on the forest dynamics could be studied. Another reason is the big importance, which is given to the site and its degree of influence on the species composition and forest development (Splechtna et al. 2005). In recent years still more and more studies refer to the importance of disturbance during dynamic formation of forest stands in the Central and Western Europe (Fischer et al. 2002). Especially the Central and Western Europe are regions where the natural disturbances and mountain forest dynamics are probably mostly caused by wind and by insect outbreak. Because of the lack of the original natural forests in this part of Europe, in which the research could be conducted not only on the level of one single stand but also on the level of countryside, it is necessary to use alternative resources (Svoboda 2008). These alternatives can be historical data of diverse origin (from historical documents to dendrochronological data).

Figure 1: Appearance of mountain spruce forest after a disturbance caused by bark beetle attack – Šumava National Park (Photo: R. Surmová)

3.3. Biological legacies

Biological legacies are defined as the organisms, organic matter (including structures), and biologically created patterns that persist from the pre-disturbance ecosystem and influence recovery processes in the post-disturbance ecosystem (Franklin et al. 2000). Legacies occur in varied forms and densities, depending upon the nature of both the disturbance and the forest ecosystem.

Biological legacies play important roles in ecosystem reorganization and in the recovery following the disturbance (Franklin et al. 2000, Franklin & MacMahon 2000). A generalized function of legacies is that of "lifeboating" or perpetuating genotypes and species in situ, which is particularly relevant to conserving biological diversity within heavily disturbed forest ecosystems (Lindenmayer & Franklin 2002). Specific mechanisms by which biological legacies “lifeboat” biological diversity include the following:

1) Perpetuating plant species, as surviving immature or mature individuals or as reproductive structures, such as seeds, spores, or vegetative parts with sprouting capability.

2) Perpetuating biota by providing habitat, supplying energy and nutrients, and by modifying microclimatic conditions.

3) Providing habitat for recolonizing organisms, primarily by structurally enriching the developing young stand.

4) Improving connectivity in the landscape for some organisms by providing protective cover within the disturbed area.

These roles are particularly prominent where a large and intense (i.e., stand replacement) disturbance has taken place, but they also occur with smaller disturbances, such as within midsize to large canopy gaps in an otherwise intact stand (Franklin J. F. et al. 2007).

A major part of the “lifeboating” function is typically provided by the larger biological structures that persist following a disturbance, such as live trees, snags, and downed boles. These structures sustain organisms in the post-disturbance environment by providing necessary habitat (e.g., nesting sites and hiding cover) and energy, especially right after the disturbance. Live green plants have particular importance in sustaining high-quality energy flows to the belowground organisms and food webs, as well as to the aboveground herbivores.

Residual structures also modify microclimate, often bringing it within the acceptable environmental range for organisms to survive (Franklin J. F. et al. 2007).

3.4. Natural regeneration

Natural regeneration is a process where an existing usually mature forest stand is being replaced by a new generation of forest stand. Not just the mountain spruce forest, but also other forest ecosystems regenerate due to the decay. Once the created forest stand, which is not to be harvested, is about to arrive to the stage of senescence where lighting and regeneration of vegetation appears (Svoboda 1952). Physiological senescence is followed-up by decay of the individual trees (Míchal et al. 1992). Nevertheless, this event happens very rarely. Due to the influence of abiotic and biotic disturbances (in the Central Europe mainly windstorms and bark beetle outbreaks) an untimely decline of mature spruce stands occur (Fisher et al. 2002, Křístek et al. 2004).

Natural regeneration, its age, species and height structure, as well as the growth and development of seedlings and saplings, plays a key role in the restoration of the tree layer of forest ecosystems in the non-management zones of protected areas. The regeneration processes and their dynamics have strong influence on the stability and functionality of forest stands. The advantage of natural regeneration is before all the keeping of autochthonal or proved local populations of forest woody plants. Another advantage is the good adaptation of seedlings and saplings on some pronounced site distinction. This enables an effective use of this site. An undisputed advantage of the natural regeneration is its undisturbed growth and development of seedlings and saplings (especially with respect to the root system) and generally higher genetic variability (higher share of heterozygotes than by artificial regeneration) of the following stand, which brings higher adaptability and immunity of the following stand (Korpel' et al. 1991).

3.4.1. Natural regeneration of Norway spruce forest

The variability of occurrence of natural regeneration in Norway spruce forest is significant also in terms of one relatively homogenous locality. Numbers of individuals differ distinctly on few meters of distance. There are differences between the regeneration in a living mature forest stand and a dead forest stand. The main difference is the amount of regeneration in the youngest age class, which is dependent very much on the close distance and high density of the mature fertile trees. The sites with the fertile mother stand can have up to ten times higher density of youngest class of regeneration than the sites with the dead stands (Ulbrichová et al. 2008).

There is not just the difference in numbers of seedlings between the natural regeneration in a living and in a dead forest stand. The height structure of the regeneration differs due to the refilling of new seedlings and also due to the higher height increment on the sites with more open canopy and better light conditions, which appears in the dead forest stand. The curve of occurrence of natural regeneration on a site with dead forest stand has a shape close to Gauss curve, while on the sites with living mature stand, which is very slightly or not at all influenced by the human activity, has the curve more or less an exponential shape (Ulbrichová et al. 2008).

The spatial structure of natural regeneration in the dead or living mature stands does not differ significantly. It is given due to the preference of seedlings germination on the suitable microsite, which leads to an aggregated spatial structure. From this point of view, the natural regeneration differs very much from the artificial one, which is placed more regularly in the space and the random design of spatial structure prevails (Ulbrichová et al. 2008).

The mountain spruce forests, which grow in a humid and cold environment, do not regenerate continually. Norway spruce (*Picea abies*) requires a period of two consecutive years with favorable temperature and humidity in order to flower and create seeds. Such a situation happens in the mountains irregularly, usually once in few years. After a seminal year tens of thousands of small spruce seedlings on 1 ha can be found. The number of small seedlings gradually decreases before a new seminal year comes and then the number starts increasing again. Norway spruce is able to recover his growth even after many decades of surviving in the form of a small seedling. Such trees, unlike trees developing in full light conditions, have very dense annual rings from this early phase of life and they can live even few centuries (Jonášová 2013).

The dieback of the tree layer is provided in natural spruce forests by disturbances. These events are caused in the conditions of the Central Europe mostly by wind and bar beetle attack. Such an event is traditionally perceived as a negative destructive calamity for the tree layer, but in context of the whole ecosystem it is not so. The disturbances are an important process not just for the Norway spruce regeneration but also for keeping the biodiversity of almost all groups of organism, which are connected with the mountain spruce forest.

4. METHODOLOGY

4.1. Locality

The data collection took place in the Šumava National Park on ten permanent research plots. These plots can be divided into two groups, according to their locality. Five of them (plots P3, P4, P5, P6 and P7) are located close to the mountain peak Trojmezná and for the purpose of this study they will be called group "Trojmezná". The other five plots (P10, P11, P12, P13 and P14) are located in the area close to the municipality Modrava and the well-known tourist place Březník. For purpose of this study these plots will be called group "Březník".

4.1.1. The habitat conditions

The group Trojmezná is situated on the northern slope of the mountain Trojmezná,in the area of the Trojmezenská hora Natural Monument in the 8th forest vegetation zone in the very cold and humid climatic region. This region has less than 10 summer days and the average day temperature during the summer is less than 12 °C, with more than 70 frost days and the average winter day temperature are under -4 °C. The annual precipitation is over 800 mm with more than 140 days with precipitation during the summer and more than 120 days with long-term snow cover during the winter (CENIA 2010). From the phytocenological point of view, this locality is classified as *Athyrio alpestris-Piceetum*, which means not very dense mountain spruce forest with *Athyrium distentifolium* (Neuhäuslová 1998).

The research plots in the group Březník are more scattered. Two of them are situated in the area of the springs of the river Vltava, and other three on the localities “U Trampusova křížku”, “Březník” and “Javoří slat”. This group of plots also belongs to the 8th forest vegetation zone, but the climatic region is cold and humid, which means 10 – 20 summer days per year, summer temperature in between 12 and 13 °C, 60-70 frost days, winter temperature in between -3 and -4 °C, the annual precipitation exceeds 800 mm, the number of summer days with precipitation is higher than 140 and the number of days with long-term snow cover is in between 80 and 120 (CENIA 2010). According to the phytocenology these localities belong mainly to the *Calamagrostio villosae-Piceetum* (mountain spruce forest with presence of *Calamagrostis villosa* in the herb layer), or *Sphagno-Piceetum* and *Bazzanio-Piceetum*, which means spruce forests on the waterlogged areas (Neuhäuslová & Eltsova 2003).

4.1.2. Historical development of the locality

The forest stands of the currently dead generation of trees in the group Trojmezná developed at the end of the 19th century, after a calamity caused by a windstorm, followed by overpopulation of bark beetle and sanitation logging in the years 1874 to 1882. Before this calamity the forest stands were evaluated as spruce monoculture virgin forests (Jelínek 1997). This means that the origin of the currently dead generation of trees at Trojmezná is connected with the effect of combination of natural calamity and sanitation logging (Svoboda & Zenáhlíková 2009).

The following development continued without any essential human intervention. The dominant tree species were spruce with admixed birch and rowan (Jelínek 1997). In the time period from 1950 until 1989 the area was inside the military border zone of Czechoslovak Socialist Republik and the intensity of management was minimal. Since then the stands were influenced by windstorms and bark beetle outbreaks and after the establishment of Šumava National Park in 1991 these stands were protected as 1st or 2nd zones, eventually as the Trojmezenská hora Natural Monument (Svoboda & Zenáhlíková 2009).

The origins of the forest stands of the currently dead generation of trees in the group Březník are more dissimilar, but in 1862 most of them were also older than 120 years. On the 18th/19th January 2007 the strong windstorm Kyrill destroyed significant part of Šumava Mountain forests and after the overpopulation of bark beetle, which followed-up, the forest stands in the areas of interest started to die (Zenáhlíková 2012). Today the stands at the areas of interest are in the process of decay.

4.2. Establishment of the research plots

The research plots were established on sites of natural forest (evaluation of naturalness according to VUKOZ) (ÚHÚL). The plots were selected according to the management maps with the precondition of non-intervention management in the localities and in the stands recently attacked by the bark beetle (*Ips typographus*). The research plots P3–P6 were established in years 2006-2007 and the research of the dynamics of regeneration began in 2008. The other 6 plots (P7 and P10-P14) were established in 2009 (Zenáhlíková 2012) (Tab. 1).

Table 1: List of the permanent research plots (Zenáhlíková 2012)

Research plot	Locality	Height above the sea level [m]	Data collection	
			2008	2009-2014
P3	Trojmezná	1275	x	x
P4	Trojmezná	1227	x	x
P5	Trojmezná	1200	x	x
P6	Trojmezná	1167	x	x
P7	Trojmezná	1353		x
P10	U Trampusova křížku	1172		x
P11	Vltava Springs	1212		x
P12	Vltava Springs	1221		x
P13	Březník	1119		x
P14	Javoří slať	1097		x

During the establishment all individuals of the tree vegetation layer were measured and localized with the technology FieldMap. The same was done with the lying logs. Each square research plot with the edge of 50 m was divided into a net of 100 smaller squares with the edge of 5 m. In all of these 5 x 5 m^2 the vegetation cover was estimated and the amount of saplings taller than 0.2 m was counted. Based on these parameters, 5 squares with the edge of 5 m from each research plot were selected. The criterion was to include the variability in presence of the dominant vegetation type and the amount of regeneration. Using the metal ribs a net of 100 smallest squares with the edge of 0.5 m was created (Fig. 1). This 0.5 x 0.5 m square is the basic unit in which the data collection about the population dynamics takes place (Zenáhlíková 2012).

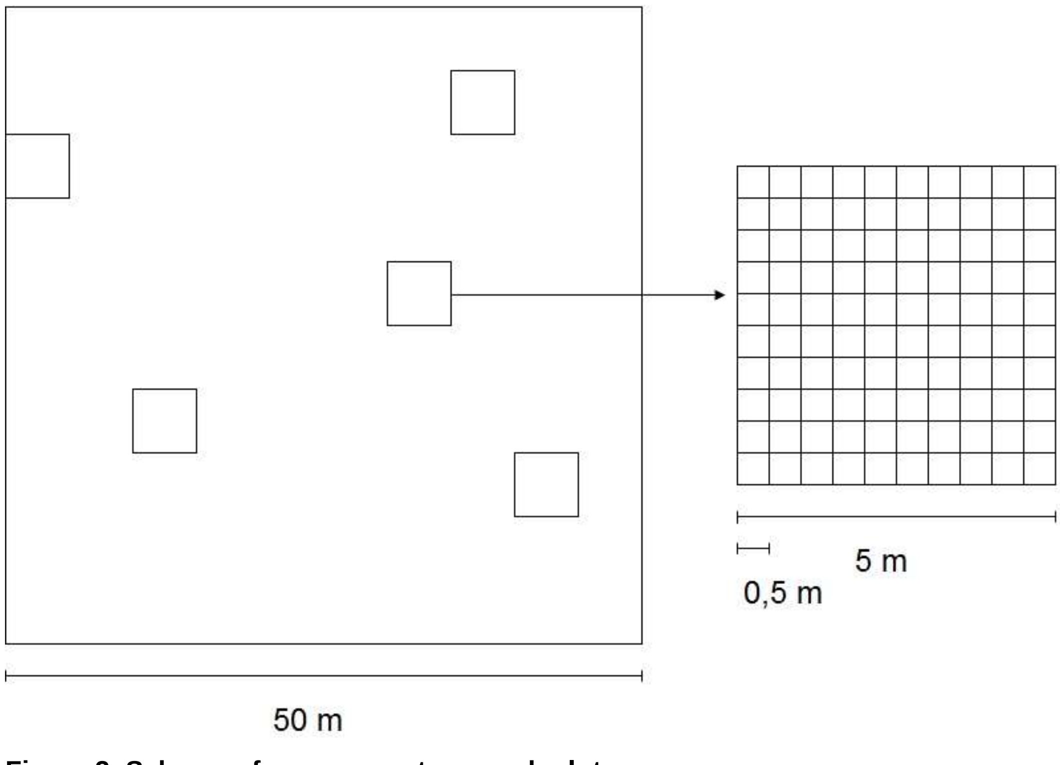


Figure 2: Scheme of a permanent research plot

4.3. Data collection

In each of the smallest squares all of the regeneration was marked and each seedling or sapling was evaluated according to its species, height, type of damage and part of the damaged individual. The microsite of the sapling was also evaluated. The following microsite categories were distinguished: litter, log, stump, bottom of a tree, windthrow, mosses, grasses, fern, bilberry and others. Also a combination of more microsites together was evaluated. All living individuals taller than 10 cm were marked by a metal plate with number. All the dead individuals of the regeneration were described same like the living and they were removed from the plot to enable the evaluation of mortality each following year. Each following year the increment of every single individual was measured with the accuracy up to millimeters. The individuals of *Sorbus aucuparia* were measured every year in their whole height because of the strong predation pressure on their species and more complicated evaluation of the increment. If any individual lost its main terminal, the reason of this was evaluated (browsing, break, dries).

The data used for this study are the results of the measurements of the years 2008 respectively 2009 up to 2013 and the data collected in July and August 2014 (measurement of the increment and mortality in 2014) (Tab. 1).

4.4. Data analysis

For the data analyses the software MS Excel, Statistika and R was used.

4.4.1. The annual increment and mortality of individuals are independent of the tree species

For analyses of this hypothesis the annual increment of each living individual of the species *Picea abies* and *Sorbus aucuparia* were compared with the Mann-Whitney U test and for the analyses of the independence of mortality according to species *Picea abies* and *Sorbus aucuparia* was used the chi-square test with the Yates correction.

4.4.2. The annual increment and mortality of individuals are independent of the microsite

According to the abundance of an individual tree species on the research plots, the size of the examined area and the variability of microsites, only individuals of *Picea abies* were taken into account for these analyses. The following microsites categories were determined: Litter, Moss, Grasses, Fern, Log, Stump, Bottom of a tree and Windthrow. Categories incurred by combination of previous microsites: Moss+litter, Moss+bottom of a tree, Moss+log, Grass+log, Litter+log, VM and Other.

In category of Moss, all the species of mosses, sphagnum and lichens were included. In the category of Grasses the grasses and grass appearance plants *Calamagrostis villosa*, *Avenella flexuosa* and *Carex canescens* were included. Ferns were represented by *Athyrium distentifolium* and *Dryopterix dilatata* (Třeský 2011). Bottom of a tree means the area of the root ramp of an individual from the old dead tree generation. Also the windthrow is associated with the "cake" of the uprooted tree of old generation. Category VM means *Vaccinium myrtillus* (bilberry). In the category Other all the difficult to determine microsites or different than previous microsites were included.

The increment of all *Picea abies* individuals was averaged for each category of microsite and shown in a graph with ascending order of microsite categories according to the height of an average increment. The mortality of all *Picea abies* individuals for each category was calculated as an equation: number of dead individuals in 2014/SUM of dead and living individuals in 2014, converted to percentage. The data were shown as a graph with descending order of microsite categories according to the share of the dead individuals.

The multiple-comparison test after Kruskal- Wallis was used for the independence of increment on the microsite and a Pearson’s chi- squared test was used for the independence of mortality on the microsite.

4.4.3. The annual mortality of individuals decreases with the height of an individual

The analysis of mortality according to the height was done only for the *Picea abies* species. The individuals were divided into height classes of 100 mm, respectively 500 mm. The mortality of individuals for each class was calculated as an equation: number of dead individuals in 2014/SUM of dead and living individuals in 2014, converted to percentage. The data were shown as a graph. A Pearson’s chi- squared test was used.

4.4.4. The annual increment is increasing with the height of an individual

This analysis was done separately for the species *Sorbus aucuparia* and *Picea abies*. The data of increment and height for each individual of the species were shown in a scatterplot and the linear regression was displayed.

4.4.5. Increment according to height of *Picea abies* on different microsites

A graph showing the increment according to height of *Picea abies* on different microsites in 2014 was created. The microsite categories were reduced to 5 main categories: Litter, Vegetation, Mosses, Wood and Other. In the category Vegetation the previous categories Fern, Grasses and VM (Vaccinium myrtillus) were included. In the category Mosses the categories Moss+litter and Moss were included. In the category Wood were included the categories of Log, Stump, Bottom of a tree, Grass+log, Litter+bottom of a tree, Litter+log, Moss+log and Moss+bottom of a tree. The category Other included in this graph the previous category Other and Windthrow. This way each living individual was entered into the graph and the linear regression for each of the 5 microsite categories was displayed.

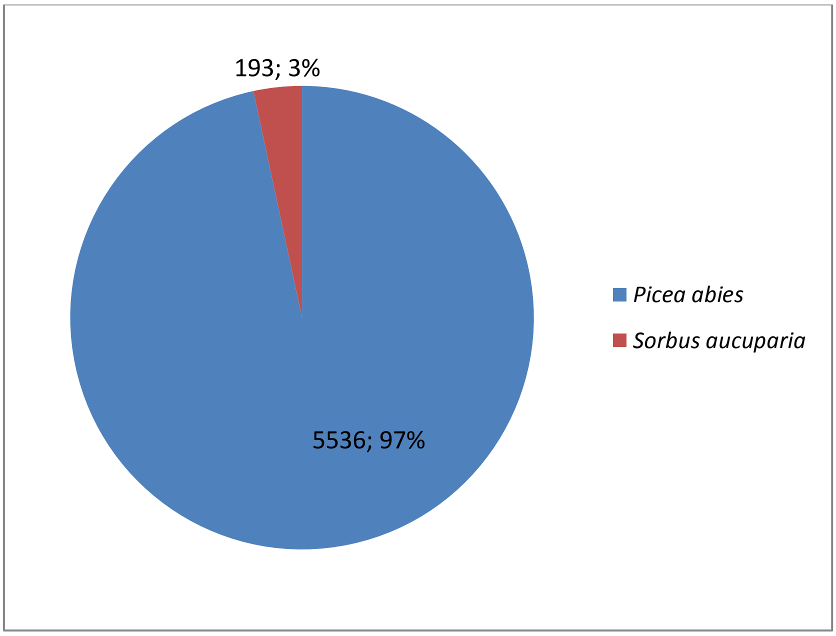
4.4.6. Mortality of individuals is caused by intraspecific competition

For this analysis only the data about *Picea abies* were used. The density of individuals was estimated with the help of the finest net of squares. For each single square with the edge of 0.5 m the number of occurring individuals was counted. According to this number the square was ordered into a density class. The following equation was calculated for each square: number of dead individuals 2014/ number of living individuals in 2013. A scatterplot as a share of dead and living individuals for each square according to the density class of the square was displayed. The linear regression was displayed.

5. RESULTS

5.1. General results

There were 4 tree species identified on the research plots. *Picea abies*, *Sorbus aucuparia*, *Abies alba* and *Salix sp.*. *Abies alba* and *Salix sp*. were evaluated as negligible (4 and 2 individuals). The dominant tree species was *Picea abies* (5 536 individuals) and the admixed species was *Sorbus aucuparia* (193 individuals) (Graph 1).

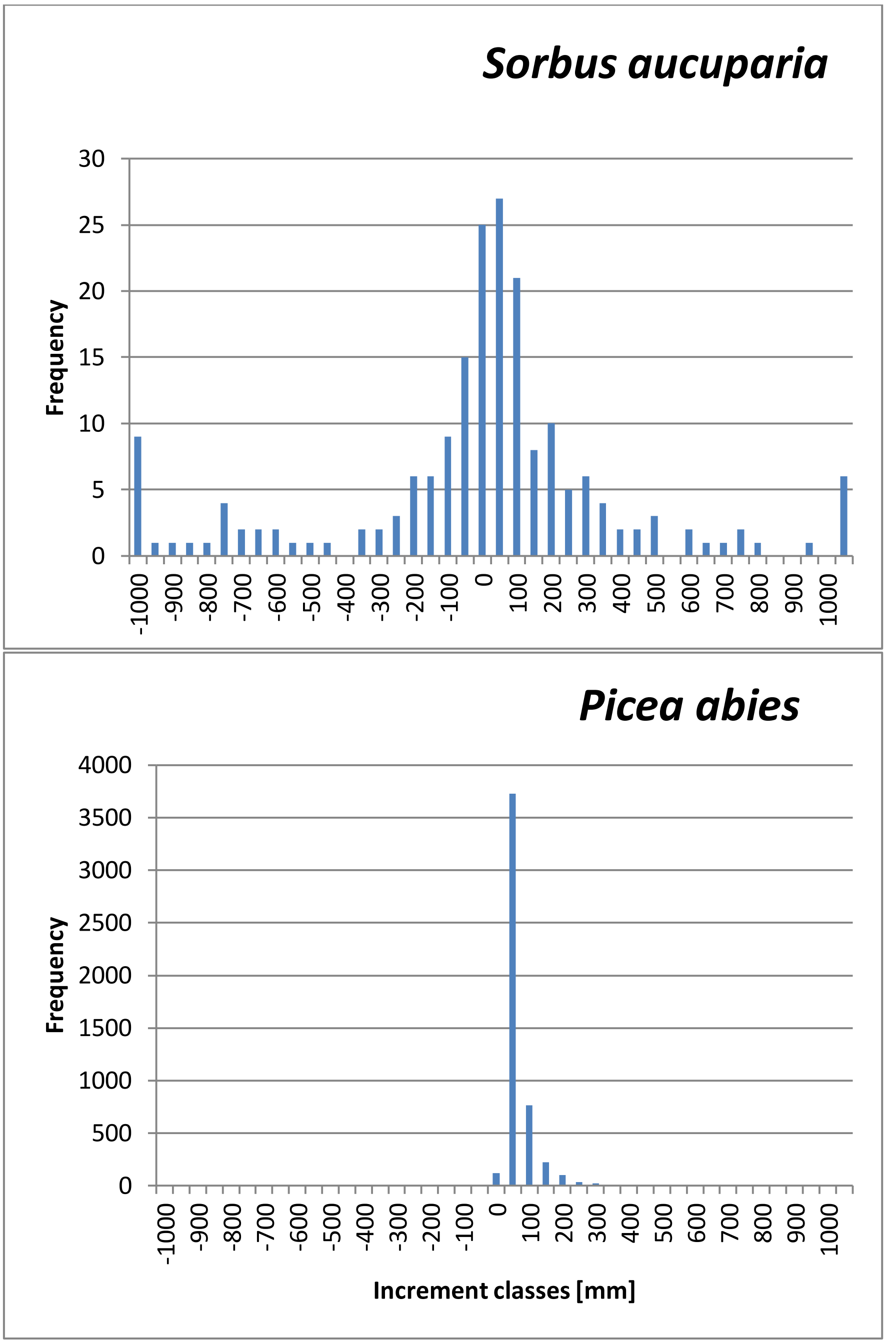


Graph 1: Proportional representation of tree species

5.2. The annual height increment and mortality of individuals depend on the tree species

The hypothesis that the annual increment of individuals is independent on the tree species was rejected ($p < 0.001$). *Picea abies* increased on the height (the average increment was 39 mm). *Sorbusa aucuparia* decreased on the height (the average increment was -29 mm). This was caused due to the massive browsing. The increment of *Sorbus aucuparia* was sometimes strongly negative, mostly correlated around zero and sometimes was strongly positive (Graph 1). The increment of *Picea abies* was centered in the range from 0 – 100 mm (Graph 2).

The hypothesis that the annual mortality of individuals is independent on the tree species was rejected ($p < 0.0038$). There were no individuals of *Sorbus aucuparia*, which died in 2014. There were 258 dead individuals of *Picea abies* found in 2014.



Graph 2: Frequency of increment [*Sorbus aucuparia* and *Picea abies*]

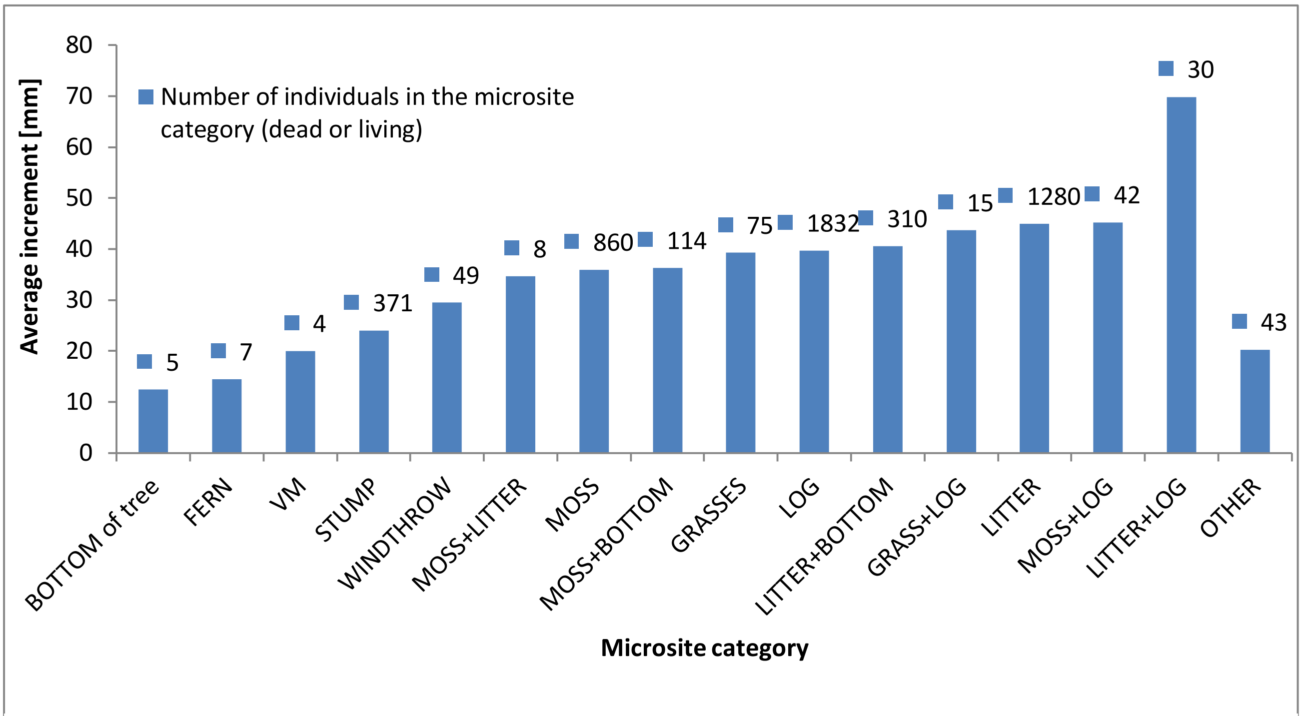
5.3. The annual height increment depends on the microsite, the mortality does not depend on the microsite

The hypothesis that the height increment of individuals is independent on the microsite was rejected ($p < 0.001$). The category pairs, which reported $p < 0.05$ were shown in the table 2. In general the microsites with log had the highest increment (Graph 3).

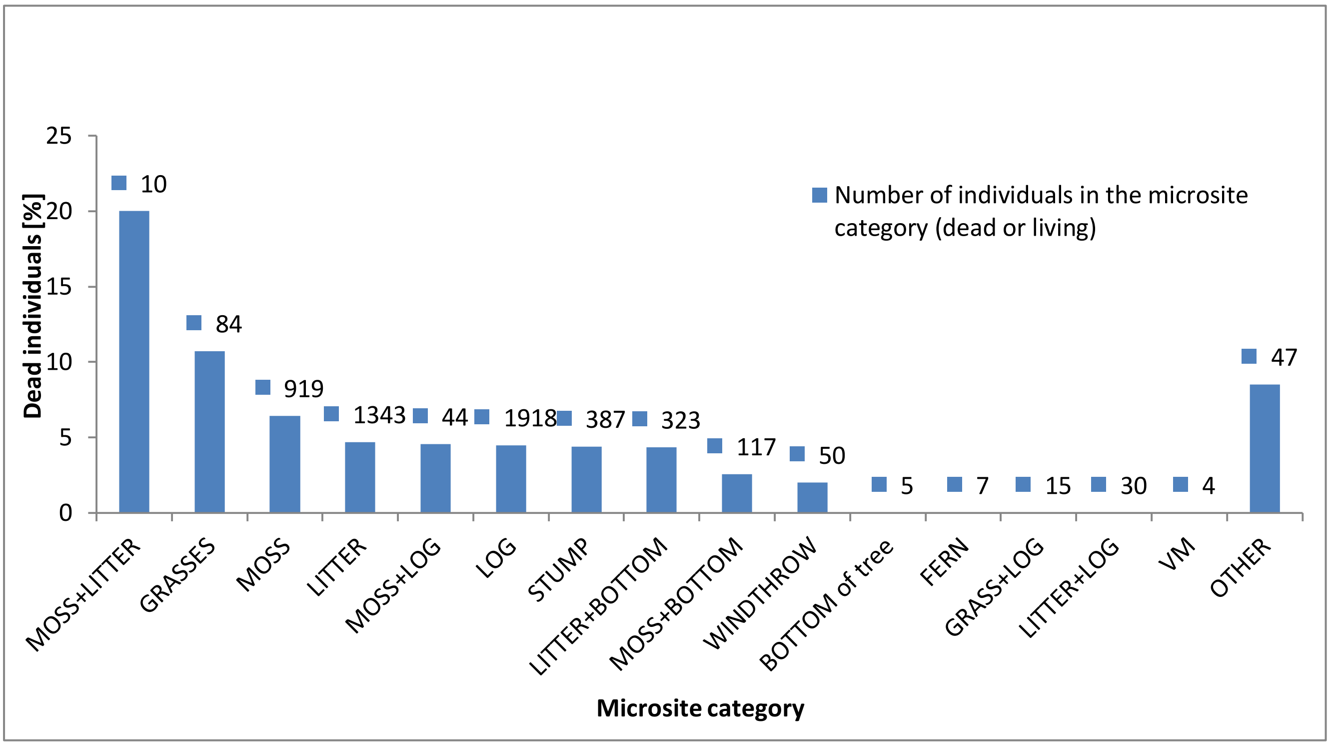
The hypothesis that mortality is independent on the microsite was not rejected ($p < 0.05$). The percentage of dead individuals in each microsite category shows the Graph 4.

Table 2: Pairs of microsite categories with significant dependence of increment

Grass+log	X	Stump	Litter+log	X	Stump
Grasses	X	Stump	Litter+log	X	Windthrow
Litter	X	Log	Log	X	Stump
Litter	X	Other	Moss	X	Stump
Litter	X	Stump	Moss+bottom	X	Stump
Litter+bottom	X	Stump	Moss+log	X	Other
Litter+log	X	Other	Moss+log	X	Stump



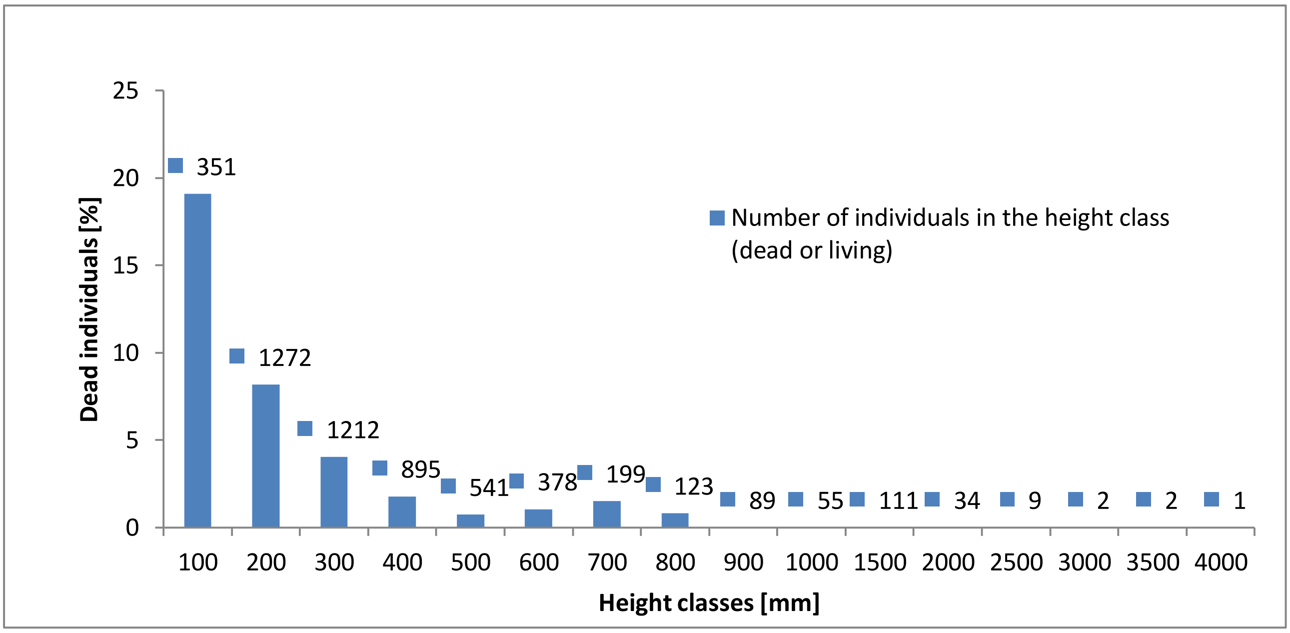
Graph 3: Increment according to microsite [*Picea abies*]



Graph 4: Mortality according to microsite [Picea abies]

5.4. The annual mortality of individuals decreases with the height of an individual

The hypothesis that the annual mortality of *Picea abies* individuals does not decrease with the height class of an individual was rejected ($p < 0.001$). The mortality was significantly descending with the height of individuals. There were close to 20% of dead individuals in the height class smaller than 100 mm. There were no dead individuals higher than 800 mm (Graph 5).

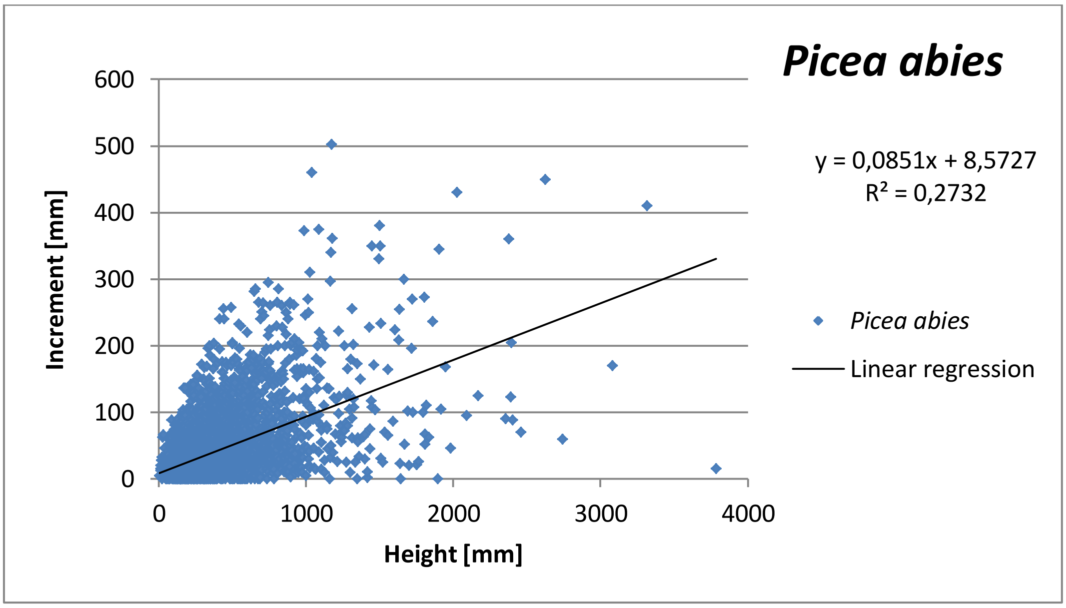


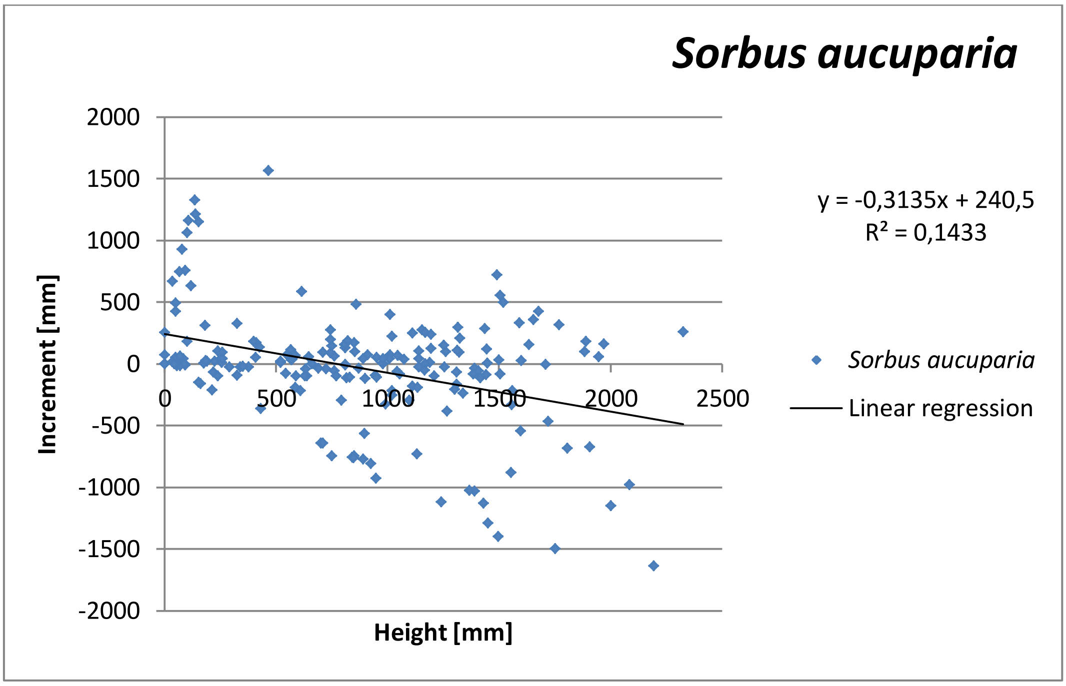
Graph 5: Mortality according to the height [*Picea abies*]

5.5. The annual height increment of an individual

According to the linear regression the increment of *Picea abies* seedling and saplings was increasing with the height of the individual. The range of increment was between 0 and 502 mm. The maximum height in 2013 was 3784 mm. The determination coefficient for the linear regression was 0.27.

The height increment of *Sorbus aucuparia* seedlings and saplings was decreasing with the height of individual, while the most common increment was around 0 mm and the range of increment was between -1642 mm and 1565 mm. The maximum height in 2013 was 2325 mm and the determination coefficient of linear regression was 0.14 (Graph 6). The negative height increment of rowan was caused due to the massive browsing, which was found by almost all individuals.

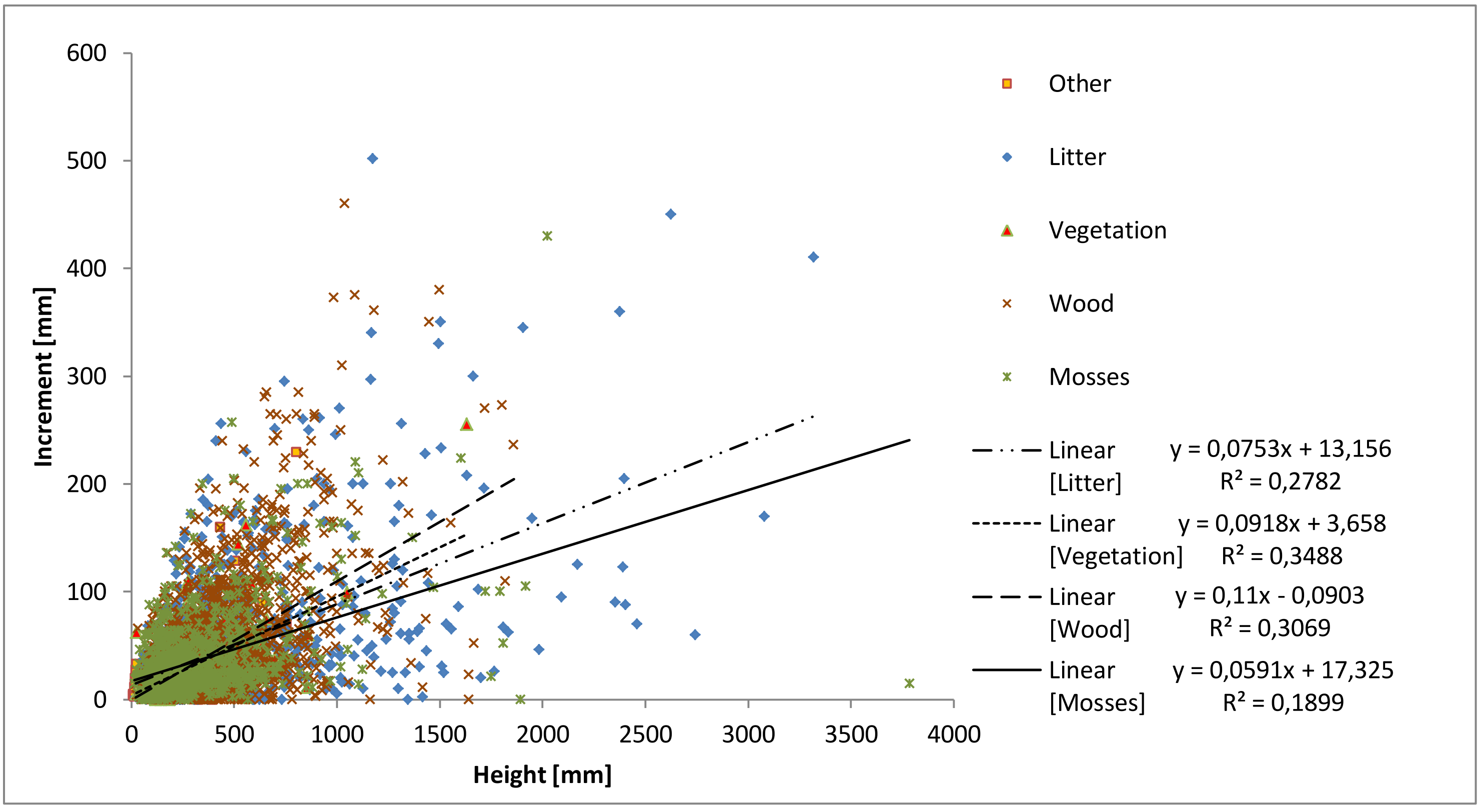




Graph 6: Increment according to the height [*Picea abies* and *Sorbus aucuparia*]

5.5.1. Increment according to the height of Picea abies on different microsites

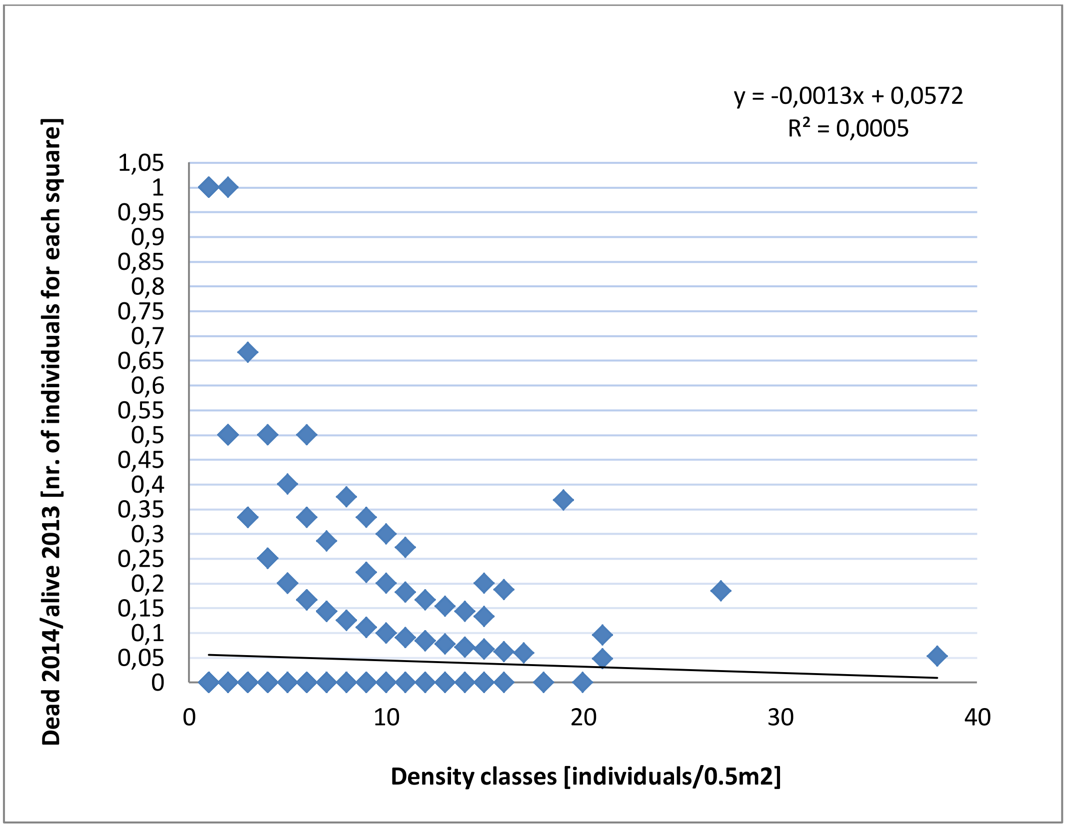
The linear regression line of the increment according to the height for reduced amount of microsite categories was most ascending for the category Wood. This was followed by category Vegetation, then Litter and the slowest ascending was the category Mosses. The coefficient of determination was 0.31 for Wood, 0.35 for vegetation 0.28 for Litter and 0.19 for Mosses (Graph 7).



Graph 7: Increment according to height of *Picea abies* on different microsites

<u>5.6. Mortality of individuals is not caused by intraspecific competition</u>

According to the linear regression the mortality was slightly descending with the higher density of individuals in the square. The coefficient of determination is very low (0.0005) and refers to negligible relationship between mortality and intraspecific competition (Graph 8).



Graph 8: Intraspecific competition of *Picea abies*

6. DISCUSSION

6.1. Influence of tree species and height of individual on the increment

The annual increment and mortality of natural regeneration in mountain spruce forest differed very much based on the tree species. The increment of *Picea abies* regeneration was clearly increasing with its height. This was probably caused by better light conditions of the highest individuals or by winning the competition with surrounding vegetation. On the other hand *Sorbus aucuparia* was damaged by browsing and its reduction was stronger with the increasing height of individual. The two present tree species (*Picea abies* and *Sorbus aucuparia*) have a different life strategy. *Sorbus aucuparia* has a huge ability to create new root shoots and sprout shoots and the original stem can be easily replaced by a new one. Rowan (similarly like spruce) also takes root even before the decline of the main spruce tree layer (Zywiec & Holeksa 2012). This strategy gives it the advantage in the competition with the herb layer, which would cause the inability of new regeneration of *Sorbus aucuparia* after the dieback of the tree layer (Holeksa 2003). *Sorbus aucuparia* is able to survive for a long time under the canopy of spruce tree layer and this gives it higher probability of survival till the canopy opening (Zywiec & Holeksa 2012). The ability of rowan creating a new stems after damage and the likely well-developed roots from the time before disturbance probably caused the zero mortality of rowan at the area of interest in 2014, even though the individuals of rowan were strongly decimated by browsing.

Browsing was the main determination factor for *Sorbus aucuparia*, which was influenced by this much more than the regeneration of *Picea abies*. This fact was also described in other studies (Bače et al. 2009, Didion et al. 2009). The hoofed game (in central Europe mainly *Servus elaphus* and *Capreolus capreolus*) causes damages by browsing and fraying. The damages can be found on small seedlings (100 mm) up to tall saplings. The most influenced individuals should measure 1100 mm (Motta 2003), which correlates with the results of this study. The high number of deer has a crucial impact on the population of *Sorbus aucuparia* and it can completely stop the growth of this species in the subalpine forests (Čermák & Mrkva 2005, Kamler et al. 2010) and boreal forests (Linder et al. 1997). According to the results of this study the growth of the rowan regeneration in the study area will probably stop, because there were huge damages caused by browsing. Intensity of browsing increased with the height of rowan individuals and it would be useful to study this process in the future research.

Browsing by ungulates is ascending with the altitude and the presence of logs causes higher pressure on the individuals of mountain spruce forest regeneration by ungulates browsing (Kupferschmid & Bugmann 2005). This is probably caused in Šumava Mountains due to the stronger behalf of *Servus elaphus* in higher altitudes*. Servus elaphus* has higher demand on the seedlings than *Capreolus capreolus* and more intense browsing of *Picea abies* regeneration in research plots with higher altitude was observed.

6.2. Influence of the microsite

Dependence of *Sorbus aucuparia* volume of the increment or mortality on microsite was not evaluated in this study. According to Jonášová& Prach (2004) the microhabitat preferences were found only in the case of spruce seedlings. Regeneration of broadleaved species was found not to be dependent on the type of the microsite.

The influence of the microsite on the natural regeneration of the mountain spruce was described by many authors (Svoboda et al. 2010, Wohlgemuth et al. 2002, Ilisson et al. 2007, Bače et al. 2011, Bače et al. 2012, Čížková et al. 2011, Kupferschmid & Bugmann 2005).

The importance of dead wood as the most favorable microsite was confirmed in this study. Dead wood quantity and its quality (level of decomposition, structure, distribution in forest, etc.) are crucial for successful natural regeneration of mountain spruce forest. Dead wood was confirmed to be an important microsite for spruce regeneration (Čížková et al. 2011). A very significant difference among evaluated wood subcategories (log, stump, bottom of tree) was not recorded in this study, while the different importance of logs and stump is mentioned in some studies. The stumps play a more important role (relative to their covered area) in terms of suitable microsites for regeneration, than the logs do (Bače et al. 2011).

In other studies is also said, that the degree of ground contact of dead wood or white-rot-causing *Armillaria* spp. presence, eventually white-rot-causing *Phellinus nigrolimitatus* presence and log diameter are positively related to seedling and sapling density. Also the type of tree death plays role in the dead wood potential. The death as a result of wind uprooting is positively related to sapling density. Conversely, the presence of brown-rot-causing *Fomitopsis pinicola* and tree death as a result of bark beetle attack is negatively related to regeneration densities (Bače et al. 2011).

The opinions on litter as a favorable microsite differ. Some authors evaluate this microsite as one of the most favorable (together with the dead wood) (Jonášová & Prach 2004, Hanssen 2002). Some other authors evaluate the presence of litter as negative for the spruce natural regeneration. Strong layer of litter can be easily affected by droughts and this can cause the difficulty for the seedlings to root into the mineral soil (Brang 1998). In this study litter was favorable microsite for the annual height increment of spruce regeneration (similar like the dead wood microsites), but it had higher mortality than the dead wood microsites. The high increment may be explained by good nutrient supply on litter microsite but the danger of death for the seedlings is probably higher due to the higher sensitiveness to droughts on this microsite.

Mosses are according to some authors described as not favorable for establishment of spruce seedlings (Valkonen & Maguire 2005). According to some other authors (Jonášová & Prach 2004) mosses were described as quite favorable microsite for seedling establishment but high mortality was registered here. In this study the height increment of seedlings and saplings on mosses was the least increasing and the mortality was high, while there were quite a lot of individuals on mosses. This corresponds with Jonášová & Prach (2004). The relative high number of seedlings on the mosses is probably related to the favorable conditions for seed germination (especially enough water). The earliest stages of growth are probably influenced by high competition of the mosses and so the mortality is high. Mosses very often cover the rocks or stones, while the soil under them is not well developed. This may by a reason for the high mortality of regeneration on mosses and low increment through the development of both seedlings and saplings.

The microsites with vegetation had very low density of regeneration, but the height increment according to height was steeper ascending than by mosses and also than by litter. This is also confirmed by the study of Jonášová & Prach (2004), where very poor amount of regeneration under grasses was described, but those individuals, which survived the competition, had no more problems with viability later on. In case of this study the individuals influenced by vegetation competition 6 years after the bark beetle attack had still high mortality.

In a research from Estonian spruce forest the microsites were evaluated from the point of view of microrelief. The result for *Picea abies* species was that the seedlings growing in the pits were smaller than those growing on the mounds (Illisson et al. 2007). Illisson et al. (2007) see the reason for small *Picea abies* seedlings in the pits in relation to the later time of establishment due to difficult environmental conditions in the pits. Clinton and Baker (2000) suggest that the reason for small *Picea abies* seedling in the pits is due to the lower light availability than on the mounds. One way or another, both of these suggestions support the possible fact that the dead wood microsite like logs or stumps have the highest increment not only because of the substrate of this microsite, but also because of their higher position in the microrelief (similarly like the mounds).

6.3. Influence of intraspecific competition

Grassi & Giannini (2005) reported about no significant competition among natural regeneration of *Picea abies* in eastern Italian Alps, which may corresponds with this study. No significant intraspecific competition 6 years after the bark beetle attack was also determined in this study. Result of the analyses does not have to mean there is no intraspecific competition at all, but the share of individuals, which died due to the intraspecific competition, was less important than the share of individuals, which died from some other reasons. There were some small groups of dead spruce individuals found in dense regeneration areas, but mortality of these individuals was probably rather caused by microhabitat influence than by intraspecific competition, while competition would probably not cause the death of relatively uniform group of individuals with similar appearance. A small portion of mortality was caused by the damage of seedlings or saplings by falling down of the decaying parts of tree stems.

.The spatial structure of the regeneration was significantly aggregated. Most of the groups were aggregated around bases of dead trees from the old generation. Wild et al. (2014) see the reason for this phenomenon in the formation of these groups before the disturbance. Seeds are “trapped” at the bases of trees in tree wells (circle spaces around the living tree in winter, where the snow cover is lower than elsewhere). Here have the seeds the best conditions for germination and later development due to the low competition with other vegetation and due to the wetness in the shade of old tree. This situation causes the “spatial pattern memory”, when the new generation of trees will later mirror the spatial structure of old the generation of trees. Some mortality due to intraspecific competition probably proceeds or will proceed, but in this phase of new stand creation

(6 years after the disturbance) is less important than the mortality caused by not favorable microsite.

7. CONCLUSION

This study confirmed the different process of Norway spruce and rowan regeneration shortly after the dieback of the tree layer of mountain spruce forest. The individuals of rowan showed zero mortality, but the pressure due to browsing was increasing with their height and in general they showed reduction of their height. The individuals of the Norway spruce showed increasing increment with their increasing height and decreasing mortality with their increasing height.

The influence of the microsite was confirmed as an important factor of the Norway spruce seedlings and saplings development. The influence of microsite was crucial in relation to height increment, but it was marginal in relation to mortality. In the process of regeneration approximately 6 years after the bark beetle attack, the dead wood was still the most favorable microsite with the highest height increment and lowest mortality. Conversely, mosses were evaluated as the least favorable microsite with the lowest height increment and high mortality. Litter was evaluated as favorable microsite for height increment but with increased eventuality of mortality. Microsites influenced by vegetation cover were evaluated as favorable for height increment but they showed high mortality.

The importance of intraspecific competition of *Picea abies* was not recorded as significant in this phase of regeneration.

For further research on the used permanent research plots, it would be worthwhile to study the development of rowan regeneration with the relationship to the game population dynamics in the area of interest. Also, a study of further development and growth of the new Norway spruce generation on these plots would be helpful for better understanding of the mountain spruce forest dynamics in conditions of the Central Europe.

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9. ANNEXES:

Annex 1: Illustration of rowan regeneration on one of the research plots (Photo: R. Surmová)

Annex 2: Illustration of data collection (Photo: R. Surmová)

Annex 3: Illustration of typical aggregated spatial structure of regeneration on one of the research plots (Photo: R. Surmová)