Growth response of Norway spruce stands surviving a major wind event

Master Thesis

submitted by

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Abstract

Natural disturbances have been increasing in frequency and severity in European mountain forests. Two underlying causes are climatic changes as well as alterations in forest structure and composition. Forest stands in Central Europe are mostly affected by wind disturbance.

Severe wind disturbance events are important to modify forest structure, spatial pattern, and successional processes in forest ecosystems. The impacts of strong winds on forest ecosystems are not limited to the area of structural stand damage, but also affect the surviving tree population. Although both positive and negative wind-induced growth changes have been observed, the functional impacts of disturbances on growth have received only limited attention in the literature to date. Consequently, these effects are widely neglected in the monitoring and economic assessment of wind disturbances for forestry.

The National Nature Reserve (NNR) Praděd region (Czech Republic), provides a good opportunity to study the role of wind disturbances on the remaining stand in a "close to nature" *Picea*-dominated mountain ecosystem in Central Europe. On November 19th 2004 was this Reserve particularly the Bílá Opava valley hit by an unprecedented windstorm disturbing a forest area of more than 7 ha.

To that end, the objectives of the study were to (i) describe the forest structure of surviving stands, (ii) test if wind damage causes either a release effect (improved growth) or a negative effect on growth in three different age classes, and (iii) what are the parameters that contribute to changes in increment after wind disturbance.

In NNR Praděd three age classes were distinguished in the remaining stand next to the windthrow area (young, mature and old). For each class two 100m x 20m transects were established. In each transect 36 trees were randomly chosen and cored (211 in total) for a dendroecological analysis. The analysis was split into two parts. In the first step an explanatory analysis was performed to obtain general information about the studied stand. The difference in terms of increment was tested before and after the storm in 2004, and appropriate predictors for a Multiple linear regression model (MLR) were selected. In the second step the MLR was performed in order to identify significant variables contributing to changes in increment.

Parameters were analysed in four groups of potential explanatory variables to control for multicollinearity. In the final selected set of explanatory variables, stand age represented the development stage, vitality became the indicator for health status, basal area of larger trees represented competition within the stand and the distance to the edge of windthrow area was used to describe the proximity to open conditions.

Over all trees (N = 211) there was a significant increase in growth by +6.7% (p = 0.004). The results thus support the hypothesis that the creation of an edge increases resource availability which, in turn, promotes overall tree growth. Although out of three age classes only old stands perform significantly better (+15.1%, p = 0.03) after the storm event in the year 2004.

The results of the MLR also indicate different responses in each age class.
Young stands were significantly influenced by vitality, on average a 16.4% growth loss (-24.4% at vitality = 0 and +8.0% for the first class), and only vitality classes 4 and 5 report (on average) a positive growth response to wind. However, vitality only explained 11.5% of the variation in increment response in the young stands. The mature age class was not significantly affected by any of the selected factors. The old stands report a significant positive growth response of +38.8% at the edge of the stand and this positive growth response is decreased by -0.6% for every meter distance from the edge of the windthrown area. The final model explained 16.8% of the variation in increment response in the old transects.

Using a tree-ring assessment approach, this work contributes to a better understanding of disturbance processes by investigating the growth response of different age classes of Norway spruce forests in the Czech Republic to a windstorm in 2004.

Key words: windstorm, growth effects, *Picea abies* (L.), release effect, edge effect

Zusammenfassung

Störungsfrequenz und –magnitude haben in europäischen Bergwäldern in den letzten Jahrzehnten deutlich zugenommen, wobei sowohl Klimawandel als auch Änderungen in Waldstruktur und –zusammensetzung zu diesem Anstieg beigetragen haben. Im mitteleuropäischen Kontext fehlen häufige Störungen durch Feuer um das Waldbild zu definieren, die Waldbestände sind hier am häufigsten von Störungen durch Wind betroffen. Starke Windstörungen sind ein wichtiger Modifikator der horizontalen und vertikalen Waldstruktur in vielen Waldökosystemen. Die Auswirkungen von starken Winden auf Waldökosysteme sind jedoch nicht nur auf den unmittelbar durch Mortalität betroffenen Bestand beschränkt, sondern haben auch umfassendeAuswirkungen auf den verbleibenden Bestand. Obwohl beides, positive als auch negative windinduzierte Wachstumsänderungen am verbleibenden Bestand beobachtet wurden, haben die funktionellen Auswirkungen von Sturmereignissen bisher nur begrenzte Aufmerksamkeit in der Literatur erhalten. Außerdem wurden diese Effekte bisher bei der Überwachung und Bewertung der wirtschaftlichen Schäden von Sturmereignissen für die Forstwirtschaft vernachlässigt.

In diesem Zusammenhang bietet die Region Nationales Naturschutzgebiet (NNR) Praděd, Tschechische Republik, eine gute Möglichkeit die Rolle von Windstörungen auf das Wachstum des verbleibenden Bestands in naturnahen, von *Picea abies* dominierten Waldökosystemen zu untersuchen. Am 19. November 2004 wurde dieses Reservat, insbesondere das Bílá Opava Tal, von einer Sturm getroffen und hat eine Waldfläche von mehr als 7 ha zerstört.

In diesem Sinne war es das Ziel dieser Arbeit (i) die Waldstruktur nach dem Windstörungsereignis im Jahr 2004 zu beschreiben, (ii) zu testen ob Windschäden zu einer Verbesserung oder Minderung des Wachstums des verbleibenden Bestands in drei verschiedenen Altersklassen beitragen und (iii) festzustellen welche Parameter für diese Zuwachsänderungen relevant sind. In NNR Praděd wurden drei Altersklassen in der Umgebung der Windwurffläche (Stangenholz, Baumholz, Altholz) unterschieden. Für jede Klasse wurden zwei 100m x 20m Transekte beprobt. In jedem Transekt wurden 36 Bäume (211 insgesamt) für die dendroökologische Analyse zufällig ausgewählt und gebohrt.

Die Analyse wurde in zwei Teilen durchgeführt. Im ersten Schritt wurde eine deskriptive Analyse durchgeführt, um allgemeine Informationen über die jeweiligen

Beständen zu erhalten. Unterschiede im Zuwachs wurden durch den Vergleich vor und nach dem Sturm im Jahr 2004 ermittelt, und geeignete erklärende Variablen aus den Bestandesdaten für ein multiples lineares Model (MLR) ausgewählt. Im zweiten Schritt wurde die MLR durchgeführt, um die signifikanten Variablen für die Veränderung des Zuwachses herauszufinden.

Die Vielzahl an möglichen Parametern wurde in vier Gruppen aus nah verwandten Variablen geteilt und jeweils die Variable mit dem höchsten Erklärungswert ausgewählt um Multikollinearität zu minimieren. Dabei beschreibt das Alter die Entwicklungsstufe des Bestandes, Vitalität ist ein Indikator für den Gesundheitszustand, die Grundfläche von größeren Bäumen (BAL) repräsentiert die Konkurrenz im Bestand und schließlich die Distanz zum durch Windwurf erzeugten Bestandesrand als Maß für die Nähe zu Freilandbedingungen.

Über alle Bäume (N = 211) wurde eine signifikante Zunahme des Wachstums von + 6.7% (p = 0,004) ermittelt. Die Ergebnisse unterstützen die Hypothese, dass die Bildung einer Windöffnung im Bestand die Verfügbarkeit von Ressourcen erhöht und das Wachstum der verbleibenden Bäume fördert. Jedoch wurde von den drei Altersklassen nur ein deutlich besseres Wachstum bei Altbeständen (+ 15.1%, p = 0.03) nach dem Sturmereignis im Jahr 2004 beobachtet.

Die Ergebnisse des MLR zeigen ebenfalls unterschiedliche Reaktionen in jeder Altersklasse. Stangenholz wurde von Vitalität maßgeblich beeinflusst, im Durchschnitt ergab dies ein Wachstumsverlust von 16.4% (-24.4% für Vitalität = 0 und + 8.0% für die erste Klasse) und nur die Vitalität der Klassen 4 und 5 zeigt (im Durchschnitt) eine positive Wachstumsreaktion auf Wind. Jedoch erklärt die Vitalität nur 11.5% der Variation im Wachstum des Stangenholzes. Die Baumholzklasse wurde von keinem der ausgewählten Faktoren signifikant beeinflusst. Das Altholz weist eine signifikant positive Wachstumsreaktion von + 38.8% an der Kante des Bestandes auf, wobei sich dieser Effekt um -0.6% pro Meter vom Rand reduziert. Das finale Modell erklärt 16.8% der Variation im Wachstum in den alten Transekten.

Die Untersuchung der Jahrringe in dieser Arbeit bietet ein besseres Verständnis der Prozesse von Störungen die eine Wachstumsreaktion in verschiedenen Altersklassen des Fichtenwaldes in der Tschechischen Republik nach einem Sturm im Jahr 2004 verursachen.

Schlagwörter: Wind, Sturm, Wachstum, *Picea abies* (L.), Störungseffekt

Certification

Hereby I, Tomáš Piatak, declare that this thesis was written by me independently without using other than indicated literature and help. All parts of the presented Master thesis, including graphs, maps, tables, etc., were acknowledged without exceptions.

Vienna, April 2015

Tomáš Piatak

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List of abbreviations and terms

Ba – Basal Area
Bal – Basal area of larger trees
Dbh – Diameter at breast height
H/D – Height / dbh ratio
HJ – Hrubý Jeseník
m.a.s.l - Metres above sea level
MF – Mountain forests
MLR - Multiple linear regression
N – Number of individuals
NNR - National Nature Reserve
NP – National Park
p – *p* value
Pcc - Pearson´s correlation coefficient
PCR - Principle component regression
PCs - Predictors
PLA – Protected landscape area
R.d.dbh – Relative dimension dbh
R.d.height – Relative dimension height
S.ratio – Slenderness ratio
St. Dev. – Standard deviation
St. error – Standard error
t - t-statistic (a ratio of the departure of an estimated parameter from its notional value and its standard error)
TSAP - Time Series And Presentation Program

1. Introduction

1.1. Ecology and management of Norway spruce in mountain regions

Norway spruce (*Picea abies* L.) is one of the most common and economically most important tree species in Europe, naturally found in the North-Western boreal zones and also in the mountain ranges of the Alps and Carpathian mountains. In the inner Alps, spruce is not limited to the subalpine belt but also dominates the montane belt. Its area has expanded far beyond the limits of its natural range. The highest coverage of Norway spruce, with more than 25% of the total land area, is found in Sweden and Austria where it covers more than 40% of the forest area (Spiecker 2000). Both countries are situated well within the natural range of the Norway spruce. A significantly high coverage of Norway spruce of 15-25% of the total land area and more than 25% of the forest land, can be found in Finland, Norway, Slovakia and Czech Republic, where spruce has often been planted within its natural range in the mountains, but also outside in hilly regions and lowlands (Spiecker, 2000). This large scale promotion of the species by management has led to many problems including the risk of increased mortality under drought conditions, relatively high susceptibility to snow, ice as well as susceptibility to fungi (Jonášová and Prach, 2004). Transformation of these coniferous stands to mixed stands is important to lower risks and represents one of the most important objectives of forest management in Europe (e.g. Spiecker 2000; Kenk and Guehne 2001; Spiecker et al. 2004).

Sustainable, multi-functional forest management in the European context is based on a “close-to-nature” concept that emphasizes the use of small-scale natural processes as a component of management, with two major benefits: (1) utilization of ecosystem dynamics that are close to those in pristine ecosystems, and (2) lower intensity of intervention efforts. In terms of scientific research great attention is always paid to forests at higher elevations (mountain forests) with focus on areas with special treatment like protected landscape areas, National Parks, National Nature Reserve (PLA, NP, NNR, etc.). Forest ecosystems are dynamic entities in time and space, their development and sustainability are shaped by disturbances (Bonan and Shugart 1989; Attiwill 1994; Frelich 2002). Natural disturbance regimes range from frequent, low-intensity disturbances creating gaps and operating on individual tree level, to infrequent, large-scale, high-intensity events (storms, insect outbreak, fires, humans) that can radically change the landscape and vegetation (Attiwill 1994; Frelich 2002; Kuuluvainen 2002; Lindenmayer et al. 2008).

The main drivers of natural disturbances affecting the dynamics and structure of forests in the central European mountain spruce forests are wind, bark beetle outbreaks and snow (Fischer et al. 2002; Schelhaas et al. 2003; Jonášová 2006; Lindenmayer et al. 2008; Steyrer et al. 2011; Svoboda et al. 2012). Over the last decades, an increase in frequency and magnitude of damages has been observed in European´s forests (Tomiczek et al. 2011). Seidl et al. (2011) suggest that between 1958 and 2001 the intensification of disturbances in Europe's forests was caused by forest change and climate change in equal measures. It was concluded that besides climatic factors, the promotion of coniferous tree species, changes in the age classes distribution, and an increase in growing stock were significant drivers contributing to an intensification of disturbance regimes in Europe in the recent past. Moreover, several studies predict a further intensification of the disturbance regime due to climate change (Lindner et al. 2010; Seidl et al. 2011b).

1.2. Wind as a dominating disturbance in mountain forests

Natural disturbances have been increasing in frequency and severity in forests around the world in recent decades (Overpeck et al. 1990; Schelhaas et. al 2003; Westerling et al. 2006; Seidl et al 2014). Initial assumptions about the dynamics of central European mountain spruce forest were described by Kulakowski and Bebi (2004), who argued that the natural variability of the forest is largely determined by strong, infrequent disturbances. In the absence of frequent disturbances by fire, forest stand disturbances are frequently driven by wind (Frelich 2002; Panayotov et al. 2011). Wind disturbance is an important modifier of forest structure, spatial pattern, and successional processes in many forest systems (Everham and Brokaw 1996). However, patterns of wind-induced damage and mortality may vary according to tree species, tree size, tree density, soil properties, landscape position, wind intensity, and wind exposure (Canham et al. 2001; Arévalo et al. 2000; Frelich 2002; Rich et al. 2007; Everham and Brokaw 1996). Based on historical evidence, severe windstorms causing stand break-up over large areas have occurred every century in central Europe (Brázdil et al. 2004; Svoboda 2006). Time period for reoccurrence of severe windstorms can be approximately 100 years at exposed sites (Zielonka and Malcher 2009; Zielonka et al. 2010) however, the mean rotation period for disturbances consisting the average value of 746 years (Thom et al. (2013). Strong windstorms cause irregularly spaced windthrows, creating gaps varying in size from the area of a single tree to several hundred hectares. The severity of a windstorm is highly influenced by storm meteorology, stand location (e.g. topography) and other factors like tree species, forest type and stage of stand development (Frelich 2002; Kulakowski and Bebi 2004; Zielonka et al. 2010). Despite these observations, knowledge about the effects of disturbances in the European mountain Norway spruce forests remains incomplete. In response, addressing the impacts of wind and other main disturbances on mountain spruce forests has become recently more pertinent (Motta et al. 1999; Nieuwenhuis and O'Connor 2001; Schelhaas et al 2003; Zielonka and Malcher 2009; Zielonka et al. 2010; Janda et al. 2010; Panayotov et al. 2011; Svoboda et al. 2010; Svoboda et al. 2012). In November 2004, a severe windstorm impacted the spruce forest stands of the Tatra National Park and damaged an area of roughly 12,600 ha (about 50 %) of the local spruce forests (Falťan et al. 2008). The same windstorm also hit forest stands in NNR Praděd in the valley called Bílá Opava (Czech Republic) and destroyed about 7ha.

The immediate impacts of such storm event on trees range from damages of individual tree compartments to total uprooting causing the dead of trees (Figure 1). Understanding these effects has been the main focus in research on wind disturbance to date.

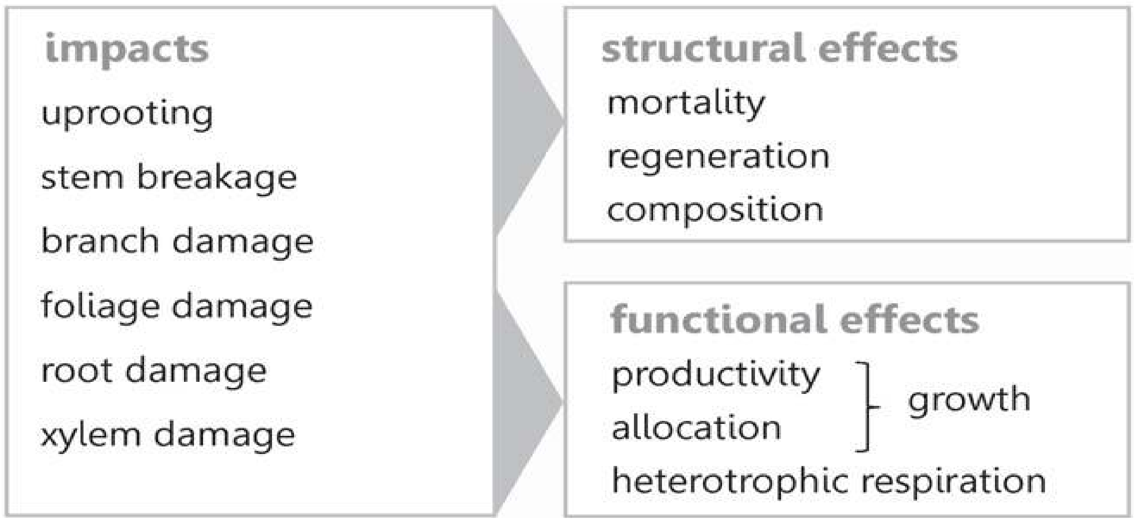


Figure 1: The impacts of strong winds and their effects on forest ecosystem structure and functioning (Seidl and Blennow 2012).

Seidl and Blennow (2012) concluded that the impact of strong winds on forest ecosystems is not limited to the immediately visible area of structural damage, but call for a broader consideration of disturbance effects including impacts on the surviving ecosystem.

Functional impacts of disturbances on growth changes after wind events, for instance, have received only limited attention in the literature. In addition, these effects are currently neglected in the monitoring and assessment of the economic damages in forestry.

These effects were studied mostly on landscape and stand level to date. Both positive and negative wind-induced growth changes have been observed. Positive effects, meaning a higher increment following wind disturbance, is mostly due to additional resources such as light, but also due to lower competition in stands (Merrens and Peart 1992; Murcia 1995; Everham and Brokaw 1996; Ueda and Shibata 2004; Zielonka and Malcher 2009; Hadley and Knapp 2011). Growth reduction, on the other hand, is a result of mechanical damage to branches, roots and xylem tissues (Nielsen; Knudsen 2004; Ueda and Shibata 2004; Seidl and Blennow 2012). Moreover these processes vary between regions and furthermore can have simultaneously positive and negative effects in the surviving tree population (Hadley and Knapp 2011).

Nevertheless the overall parameters contributing to change in functional effects are still unresolved.

2. Objectives and Hypotheses

The overall aim of this study was to assess the impact of wind disturbance on the tree growth in surviving forest ecosystems. For this purpose a wind disturbance event from the year 2004 at the National Nature Reserve Praděd (CZ) will be analysed as a case study in order to:

describe the forest structure after the wind disturbance event and analyse if the wind damage caused:

i. a release effect (i.e., improve the tree growth), or
ii. a negative effect on growth of the surviving population

In particular, the aim was to determine how these effects are related to:

iii. the distance from the edge with the windthrown area
iv. predictors of development stage, health and competition

Based on the literature review following hypotheses were formulated in relation to these objectives:

1)

a) The creation of a gap caused by a storm event decrease the competition which in turn promotes growth response resulting in higher increments (Merrens and Peart 1992; Murcia 1995; Everham and Brokaw 1996; Zielonka and Malcher 2009).

b) The alternative hypothesis is: The remaining trees after a storm event show a decrease in growth due to mechanical damage to branches, roots and xylem tissues (Nielsen and Knudsen 2004; Ueda and Shibata 2004; Seidl and Blennow 2012).

A release effect of the remaining trees is assumed to be greatest on the edge of the newly created gap and decreases with distance from the gap (Oosterhorn and Kappelle 2000; Powell and Lindquist 2011).

2)

a) It is hypothesized that the increment response after wind disturbance is positively correlated with competition but negatively with diameter and height (Szwagrzyk and Szewczyk 2001; Vizcaíno-Palomar et al. 2014).
b) There is higher response of individuals with better vitality, while vitality is a crucial factor for surviving the effect of stress (Larcher 2001).
c) Older trees tend to be less efficient to use increasing resource levels and moreover according to their bigger crown architecture are more prone to wind damage in the crown and roots. Due to the physiological effects mentioned above and competition, the release effect is hypothesized to be stronger in young than in mature and old stands (James 2010; Kaźmierczak and Jędraszak 2014).

3. Materials and Methods

3.1. Site description - Location

The National Nature Reserve (NNR) Praděd is situated in the highest parts of the mountain region “Hrubý Jeseník” on 2,031.40 hectares in north-eastern part of the Czech Republic (Figure 2). A NNR is defined as a small area of concentrated natural value typical for a particular geographic area (§ 28 par. of 1. Law, Ministry of the Environment).

Banaš and Hošek (1998) characterized NNR Praděd as an uncommon mountain and alpine ecosystems of exceptional natural value.

The reserve spreads over elevations from 820 to 1491 m, and is dominated by Norway spruce (*P. abies*) characterized by the ecotype with a specific narrow conical crown and slanted branches typical for mountain spruce forest types. These forest stands are considered near-natural forests according to the Natural Forests Databank of the Czech Republic. Main plant communities are *Calamagrostio villosae-Piceetum* with dominant *Vaccinium myrtillus* combined with *Athyrium distentifolium, Blechnum spicant* in the undergrowth (Vrška et al. 2004). Other plants of high conservation value can occur in the valley as *Viola biflora* or *Rosa pendulina* and many other plants (Natura Bohemica 2008).

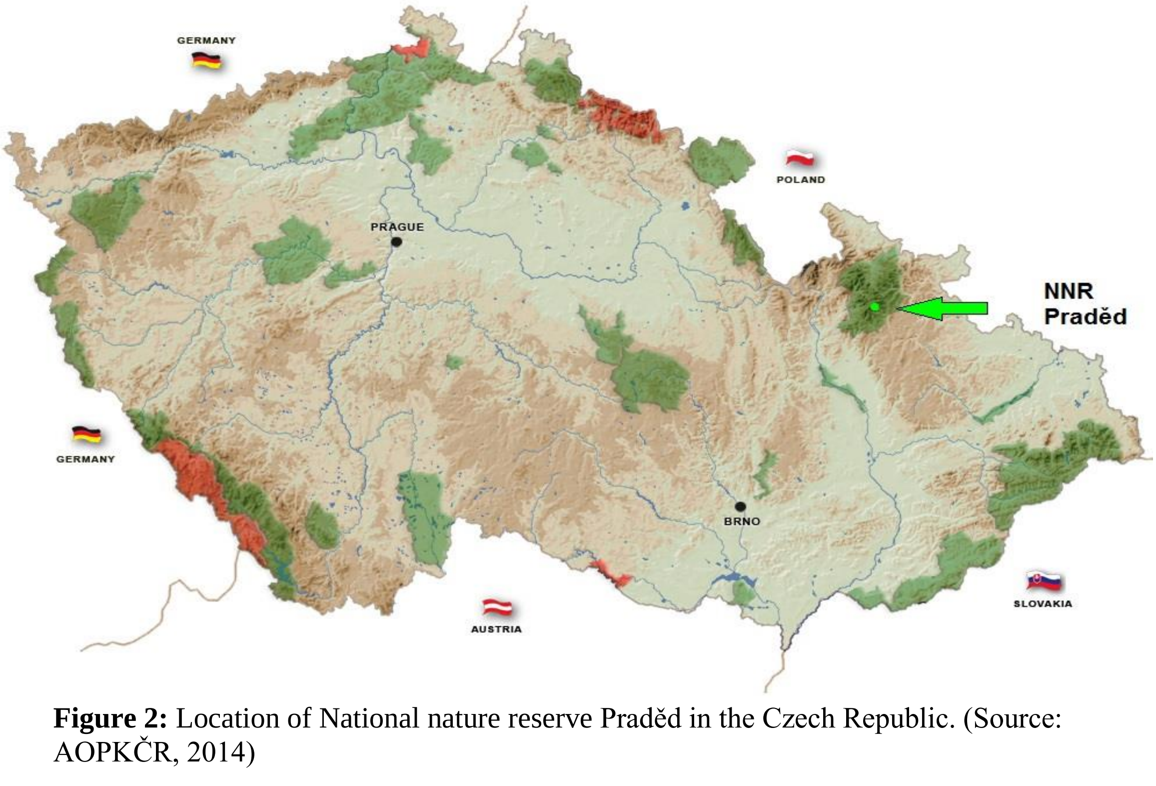


Figure 2: Location of National nature reserve Praděd in the Czech Republic. (Source: AOPKČR, 2014)

3.2. Climate

The “Hrubý Jeseník” (HJ) Mountains lies on the boundary of two climatic zones. The western boundary of the continental climate meets a lingering impact of climate Atlantic. Quitt (1971) characterized the region by a high relative humidity and the prevailing westerly winds which bring significant amounts of rainfall. Higher altitudes of HJ are classified as a cold while the other “lower” territory belongs to a slightly warm, average temperatures in summer ranging between 14-16 ° C, while the Mountainous combs belong to the coldest areas in the country. The climate diagram (Figure 3.) shows the observed average, maximum ,minimum and extreme values of temperatures (Meteoblue, 2014).

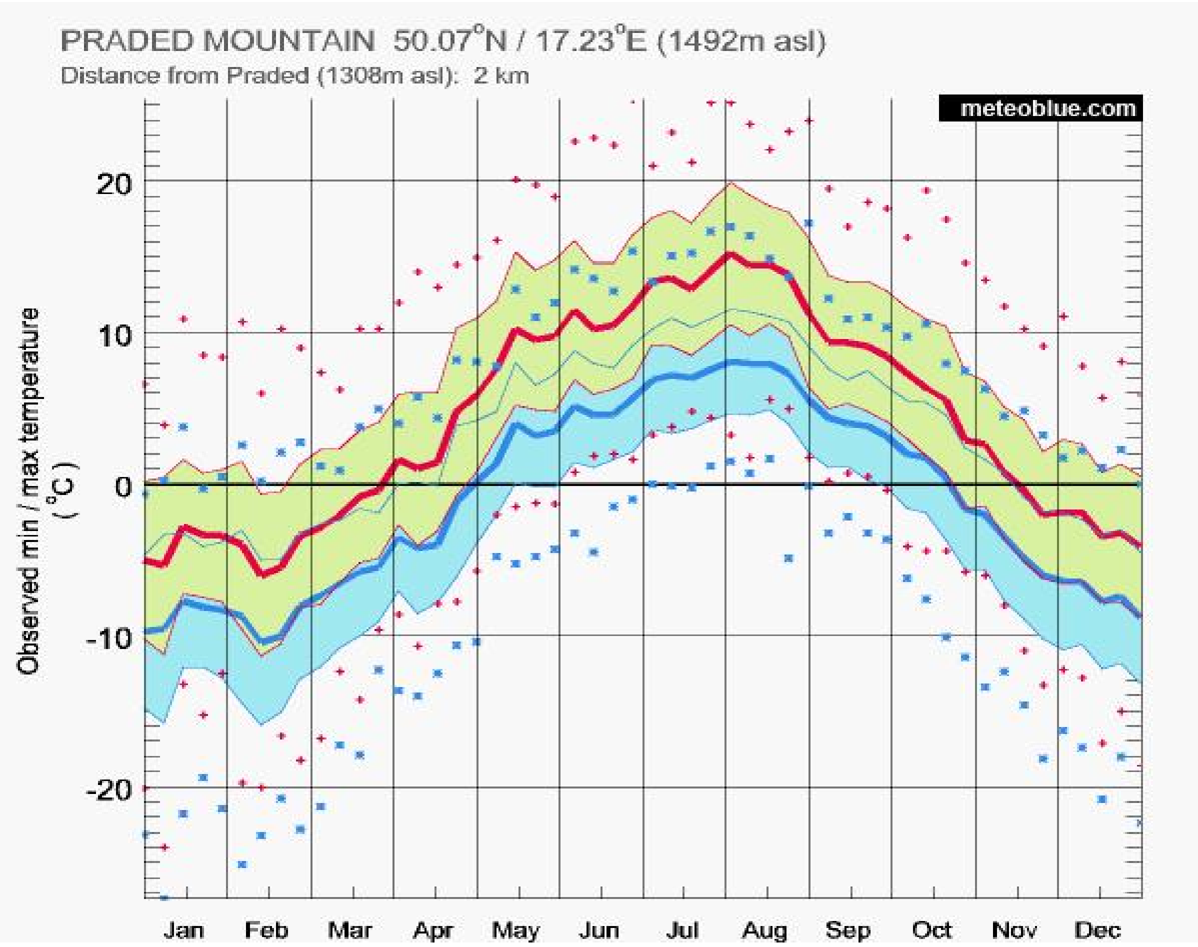


Figure 3: Climate diagram shows the maximum (red) and minimum (blue) temperatures in NNR Praděd. Extreme values are shown by + and * characters. Average values are between red and blue lines. Two thirds of the observed temperature values lie within the coloured temperature range (Source: Meteoblue, 2014).

Data came from the closest weather station Ovčárna (1308 m n. m.). Mt Praděd has an average annual precipitation in higher altitudes of more than 1250 mm and in the lower elevations of about 850 mm per year. The snow cover lasts from 100 to 140 days (the longest on the northern slopes of Mt. Praděd) Fig. 4 shows the wind speed measured at weather station Ovčárna.

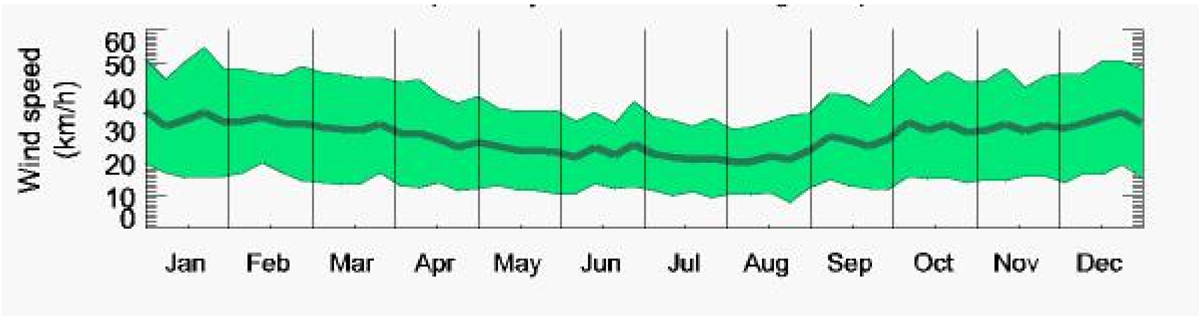


Figure 4: Diagram shows daily mean wind speed values over the whole year in NNR Praděd (dark green). Lighter green values represent the range interval of weekly means Source: Meteoblue, 2014).

3.3. Geology and Soils

Current landforms of local relief depend mainly on the tectonic evolution, geological structure and resistance of rocks to weathering and erosion. The main features of the current landscape were formed in the late Tertiary but the development continued into the Quaternary. An essential role has been played by tectonic movements - lifting and lowering the individual plates in the Tertiary, followed by erosion of running water and the activity of the glaciers but its development continued in the Quaternary (Olympia 1991).
The bedrock constitutes of chlorite – sericite phyllite and quartzite (Banaš et al. 2001), and the main soil type was classified as modal podsol according by the Czech Geological Survey (Čgs 2015). Soil is usually moderately deep to deep, sandy loam to loamy, darker colored with relatively good sorption capacity and relatively high is also biological activity. Humus form is moder. The content of the skeleton varies between 20-40%. The soil is partly wet but dries out occasionally, furthermore soil reaction is slightly acidic (AOPKČR 2014).

3.4. Historical and present use

The four national nature reserves (NPR) - Praděd, Šerák-Keprník, Rašeliniště Skřítek and Rejvíz represent together the most valuable parts of nature in HJ Mountains. Whole region is additionally subdivided into four zones of protection (for more information see appendix).

The NNR Praděd was founded in 1991 by connecting six already existing Reservations established in 1955: Vrchol Pradědu, Velká kotlina, Malá kotlina, Petrovy kameny, Divoký důl and Bílá Opava (in 1963). Currently the NNR is component of PLA of the HJ Mountains.

Historical documents of these Mountains from 1857 indicate proportions of forest type 24% for beech forest, 48% mixed forests with prevalence of beech and the remaining 28% with the spruce dominance. In the 50s of the 20th century spruce forests occupied already 65% of the HJ Mountains (Duha 2002). After the Second World War artificial restocking with unsuitable ecotypes of Norway spruce also in higher altitudes was common practice. Further expansion of clear cutting followed by frequent windstorms resulted in fragmentation of the contiguous mountain forest and its microclimate in the second half of the 20th century (Novák et al. 2010).

The high elevation areas were also affected also by pastoralism in combination with grubbing, burning and litter raking. Such activities started in the 17th century and had their highest extent in the 19th and the first half of the 20th century (Banaš et al. 2001), causing an extension of the original mountain clearings and partially reduce the upper limit of the timber line. Nowadays the tree composition of the whole Protected Landscape Area in each of the four protected zones is strongly dominated by spruce. The first zone is represented with proportion of 92%, 91% was defined in the second zone. The third zone consists of 79% spruce and the fourth zone is represented with 84% (Duha 2002). Nevertheless the NNR Praděd still serves as a genetic base for seed collection of the mountain spruce ecotype.

3.5. Sampling design

The study plots were located in the NNR Praděd in the north-eastern part of the Czech Republic in the Hrubý Jeseník Mountains at an elevation of 1100-1200 m a.s.l. On November 19th 2004, the Bílá Opava valley was hit by an unprecedented windstorm disturbing a forest area of more than 7 ha. The wind gust speed exceeded 115km/h (Tanap 2005). The same storm shortly afterwards hit the Tatra Mountains and destroyed area of 12,600 ha (Tanap 2005). The broken and uprooted trees were partly removed from the stand (approximately 50%) and the remaining individuals were debarked for phytosanitary reasons. The plots were established next to the affected areas, with transects approximately following contour lines in order to ensure comparable wind exposure (Figure 5.).

Three age classes were distinguished in the neighbourhood of the windthrow (young, mature and old). For each class two 100m x 20m transects were sampled (Figure 6.). The transects were additionally divided into two sectors. The full record of transects including the individual distribution of trees with the stands can be found in the Appendix.

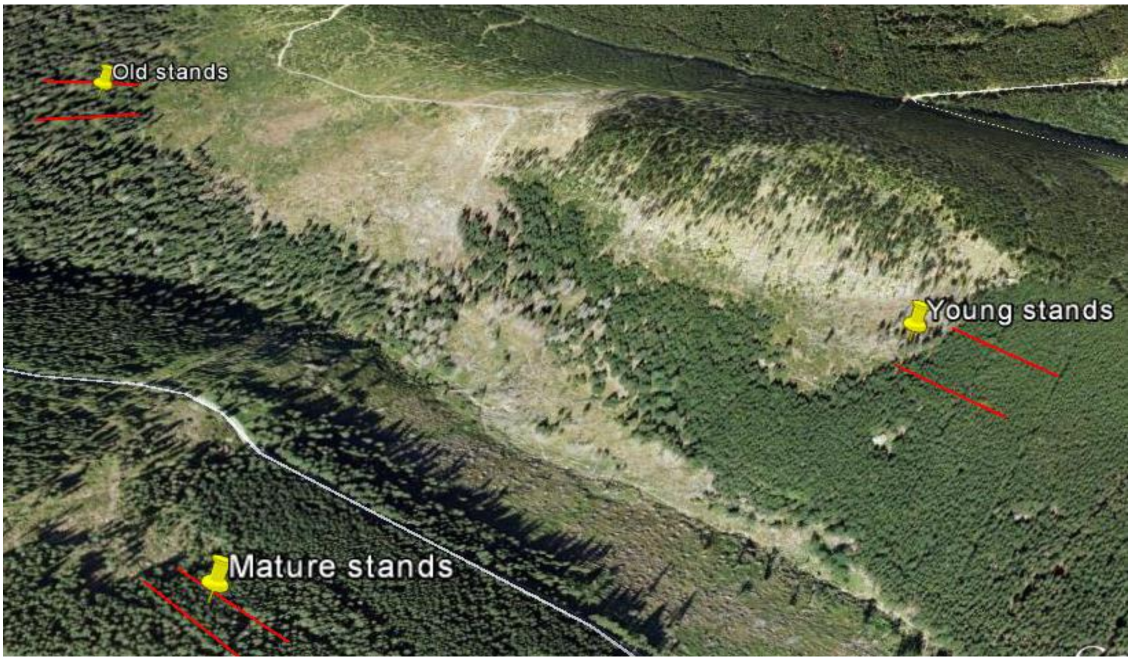


Figure 5: Location of the transects in the old, mature and young age classes NNR Praděd.

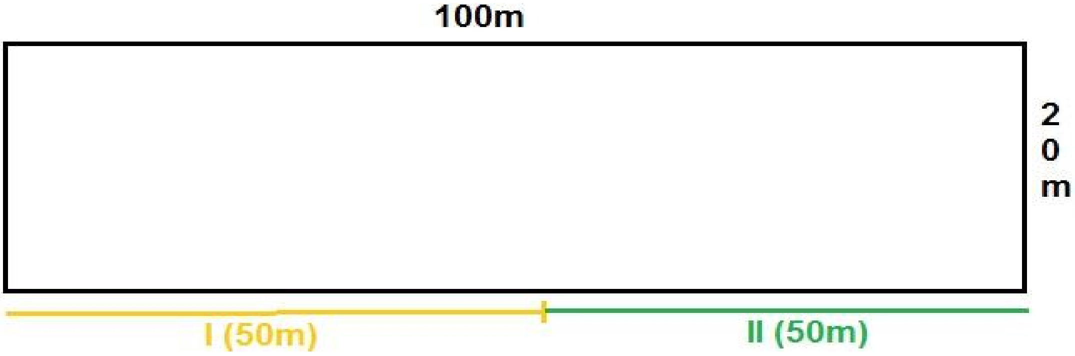


Figure 6: Design of the transects and its subdivision into two sectors.

3.5.1. Field methods

All trees with a dbh of >7 cm were investigated on the 2000m^2 sized transects, measuring their accurate position and dbh. In the first sector (0-50m) 24 and in the second part (50-100m) twelve individuals (36 in total) per transect were chosen randomly for supplementary measurement of height, crown length, stem damage, vitality and increment cores (Ø 5mm). For selecting these trees, numbers were randomly pulled out of a bag after a full cruise of the respective sector.

For more details see the Data sampling form (Appendix). A selection of trees (22) was also cored from two sides in order to test if the direction of coring plays a significant role in determining their growth response. Standing and fallen deadwood > 10 cm dbh (1,3m distance from thicker end) was also recorded within the whole transect.

Additionally general characteristics such as altitude, aspect, slope, exposition and canopy closure were described for each transect.

Specific polygons were shown with all observed trees including dead trees (R Core Team 2013) in attachment (Figures: 19-24).

For field work the following equipment was used (Figure 7.):

GPS, Vertex IV, Π – band, compass, increment driller, straws, labels with numbers, wooden spacer bars

Figure 7: Equipment used for data sampling

For clarifying the stands the slenderness ratio was calculated. Slenderness ratio is regarded as one of the tree stability criteria, and its average is used as a measure of stand stability. It was calculated by dividing the tree height (m) to its diameter (cm) at breast height (Grochowski 1973; Causton 1985; Bruchwald 1999; Jaworski 2004). Slenderness is also an indicator of tree resistance to damage caused by snow and wind. As a reference characteristic for determination of physiological predispositions to be affected by potential windstorm the following scale of values for conifers proposed by Burschel and Huss (1997) was adopted:

tree very unstable - above 1.00

unstable trees - from 0.80 to 1.00

stable trees - below 0.80

trees growing in isolation (single) - below 0.4

In the field several potential explanatory variables, like dbh, height, vitality, age and crown length, were measured. Further the parameters basal area, basal area of larger trees, relative dimension dbh, relative dimension height, distance to the edge and distance to the nearest neighbour were derived to include a wide range of different potential effects in the analysis. Yet, many of these variables are highly correlated and describe related characteristics of an individual. To mitigate the effect of colinearity potential variables were dived into four groups: development stage, health, competition, distance

3.5.1.1. Development stage – variables

As the title suggests, this group consists of variables related to physiological state of particular tree. Dbh was measured with Π – Band at 1,3m at the side of the hill. Height was measured with Vertex IV and finally particular age was determined in the laboratory by counting tree rings (see chapter 3.5.2).

3.5.1.2. Health - variables

As parameters describing health of an individual tree vitality and crown length were recorded. Crown length (in %) was derived as the proportion of the live crown to the total height of the tree.

A qualitative assessment of vitality was done for all individuals chosen for coring based on the school grading system:

1. Excellent – high vitality (healthy and symmetric green crown, no stem damage, without visible fungi and tumors)
2. Good - slight deterioration of vitality (full green crown, reduced length of crown, no fungi, no tumors, no stem cracks or damages but around still healthier trees)

3. Adequate - Evident deficiencies in vitality (drying of the crown, small stem cracks)
4. Sufficient - Significantly reduced vitality (evident crown retreat, dead top of the crown, trunk cracks, slightly uneven trunk)
5. Bad - low vitality (the greater part of the crown is dead, cracks on the trunk, visible resin flow, fungi, tumors)

3.5.1.3. Competition – variables

Basal area (ba), basal area of larger trees (bal), relative dimension dbh (r.d.dbh), relative dimension height (r.d.height) and distance to the nearest neighbour. There is no need to characterize the first four variables in this group. Distance to the nearest neighbour was calculated automatically from a database of all trees recorded in a particular transect (R Core Team 2013).

3.5.1.4. Distance - variables

The fourth group of potential explanatory variables consisted of only one parameter - distance to the edge of the windthrown area. Distance to the edge was calculated from the data set of all trees recorded in the respective transect (R Core Team 2013).

3.5.2. Laboratory methods

The cored tree ring samples were processed according to Pilcher (1990). Ring width was measured using the measuring linear table Lintab (Rinntech, Heidelberg, Germany) and the raw data processed using the Time Series And Presentation Program TSAP. To derive the complete age, where the pith was not reached exactly, the missing years were estimated by using a circle pattern from Bräker (1981). Regarding the fact that *Picea abies* regeneration can persist for decades in shade and therefore it is difficult to assess the year of germination (Niklasson 2002), it was assumed in the terms of relevant age that the work will be done with recruitment ages.

The individual raw increment curves were at first checked visually and then compared to mean local growth curves provided by the Faculty of Forestry and Wood Technology of the Czech University of Life Sciences in order to fit certain curves to relevant negative years (2004, 1996, 1980 etc.) in NNR Praděd (Figure 8.). Due to the natural decline in ring width with increasing age of the tree it is usually required to de-trend each sample before analysing the tree-ring series (Cook et al. 1990). As age-dependent growth trends may affect the results de-trending essential especially in cases where the samples contain uneven age distribution. The age trend was removed in the program TSAP. The raw data were processed in two steps. First, the age trend was removed by exponential regression. We have chosen exponential regression as the most biologically realistic variant. The program TSAP is offering generally three options. The first one is already mentioned exponential regression (Figure 9.). The second one, called Moving average, gives proper smooth results, but also removes parts of the signal we are interested in. The linear regression was excluded due to the fact, that growth of trees is not a linear function.

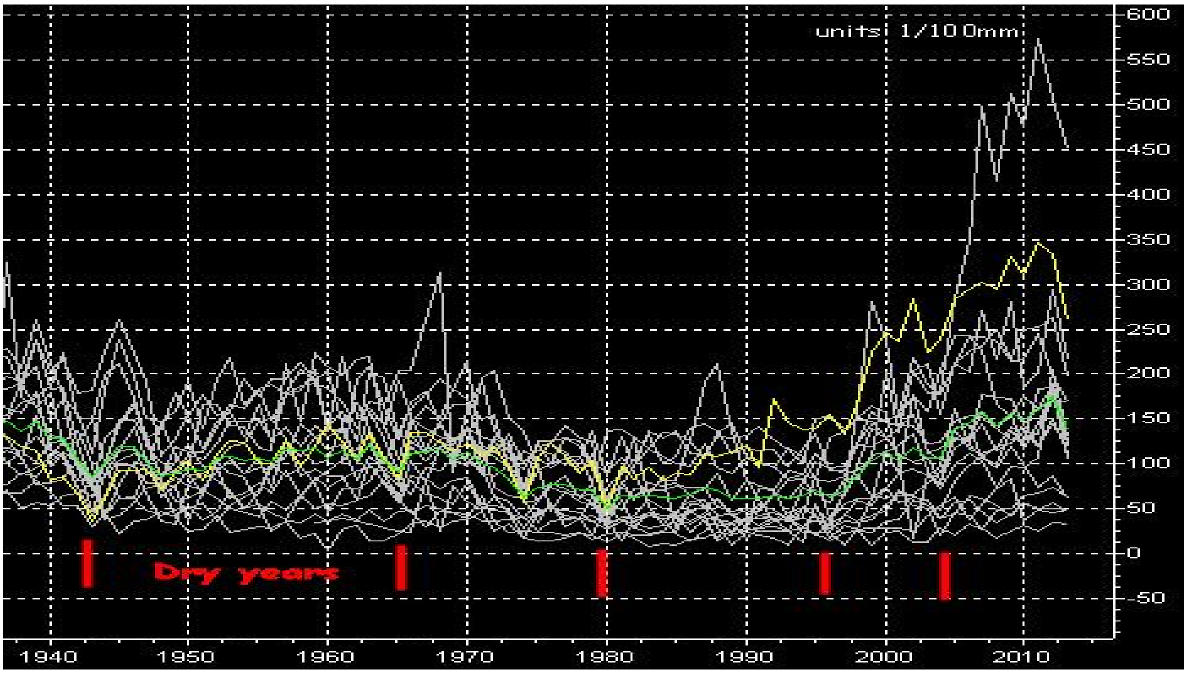


Figure 8: Relevant negative (extra dry) years in the Old stands in NNR Praděd (2004, 1996, and 1980). N=67, Red – negative years, Green – mean Growth curve, units are 1/100mm, not

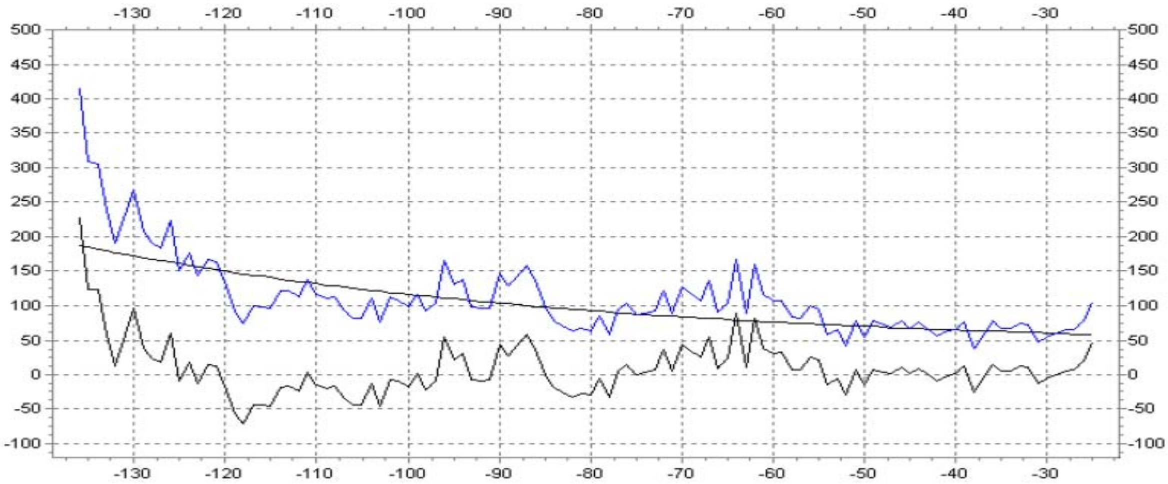


Figure 9: Example of application the Exponential regression method in TSAP chosen for de-trending of the samples. The blue curve represents original data, while the black curve is the data after removing the age trend. Units – 1/100mm

TSAP calculates an exponential regression using the following equation (i):

$$y_{i=} a * e^{b*x_i} + c \qquad \text{(i)}$$

The second step of indexation was to transform the original values (1/100mm) to relative units (percent). TSAP provides this option, where the relative units are equal to one hundred times original value divided by value of detrended series following this equation (ii):

$$r_i = 100 * \frac{a_i}{t_i} \qquad \text{(ii)}$$

a_i – Original value for year i

t_i – Value of detrended series

The index averages of nine, five and three years before and after the storm event (1996-2004 / 2005-2013) were calculated for each tree separately. This approach was chosen in order to diminish the influence of good and bad years in terms of growing condition. The growth response to wind disturbance is calculated as the index value after storm minus the value before the event divided by the value before, times one hundred. For more information see following equation (iii):

$$\Delta i = 100 * \frac{(a-b)}{b} \quad \text{a – after storm} \quad \text{b – before storm} \qquad \text{(iii)}$$

An exploratory analysis of the three averaging periods led to the decision to choose 5 year averages as an input for the analysis. This choice was mostly based on the fact of decreasing intensity of the growth response signals at the level of 9 year averages. Three years values were rejected because of a too low number of years and consequently a considerable influence of the dry year 2004. Nevertheless Panayotov et al. (2011) investigated response of old Norway spruce-dominated forest in Bulgaria to wind disturbance. They found moderate growth suppressions within first five years and only 30% of individuals reported a release effect, while during the period five to ten years after windstorm, 84% of all samples displayed releases.

3.5.3. Statistical methods

Descriptive statistics were done in order to calculate parameters like maximum, minimum and mean values, standard error and also to check for normality of the data, in order to choose further statistical methods and check for compliance with their prerequisites.

T-tests for paired samples were used to determine whether there is a significant difference between cores taken from the sides of an individual tree. All sampled trees (N=211) were pooled together and tested against the null hypothesis that there is no growth effect after wind disturbance (t-test), and subsequently if wind disturbance caused either a release effect (i.e. improved tree growth) or a negative effect on growth of the trees in the remaining stands. Each age class was tested separately to find out if there were differences in the in three different age classes. Each age class was analysed by the data from the two transects pooled together. A t-test was also used to compare other parameters like vitality, bal etc. in terms of variance between the first 50m of transects and second 50m.

All variables measured in the field were divided into four groups (see chapter Field methods 3.5.1) For each group was chosen one parameter representing particular group (

development stage, health and competition) These arrangements should help to reduce multicollinearity in the model of multiple linear regression.

Correlation coefficients between potential predictors were calculated in Statistica 12 using Pearson´s formula. Strength of relationship was split into four groups: Strong, Moderate, Weak, None or very weak (Table 1).

Table 1: Strength of relationship between correlation coefficients.

Strength of relationship	Value of r
Strong	-1.0 to -0.5 or 1.0 to 0.5
Moderate	-0.5 to -0.3 or 0.3 to 0.5
Weak	-0.3 to -0.1 or 0.1 to 0.3
None or very weak	-0.1 to 0.1

Finally, the factors contributing to the observed variation in growth responses were determined by means of regression analysis.

Regression analysis is a common and powerful analysis method when both the response variable and the explanatory variable(s) are continuous (Crowley 2007).

Generally regression analysis is a statistical tool for evaluating the relationship of one or more independent variables X1, X2....Xn with a single, continuous dependent variable Y (Kleinbaum et al. 2014). Regression analysis with backward selection based on p-values was applied (for each age class separately) on de-trended standardized samples to determine significant effects of particular explanatory variables on increment response after wind disturbance.

The analysis was started with all four variables (i.e., the full model); the one with the highest p-value was rejected and the model was fitted again until only significant variables at 95% stayed (Figure 10).

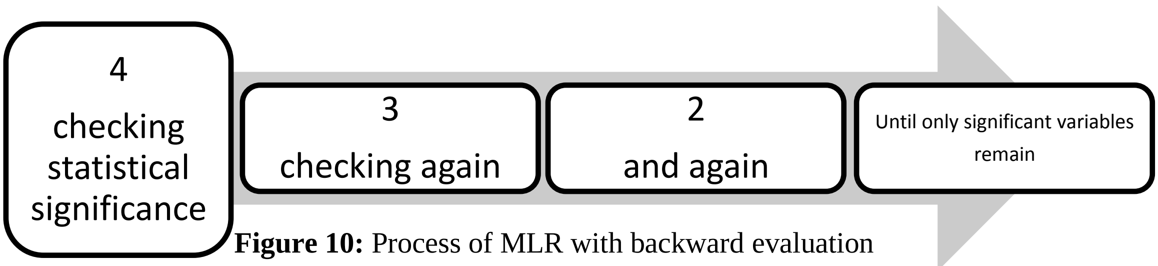


Figure 10: Process of MLR with backward evaluation

4. Results

4.1. Descriptive analysis of forest structure

General information about particular stand can be found in Table 2. Transect with a mean age of 49±12 (mean ± standard deviation) were called young with age range between 40 and 70. The mature stands had a mean age of 115±16 and the range of individual tree ages was between 110 and 140 years. Trees in the old transect had a mean age 141±40. The old stands are in terms of age more evenly distributed than the younger stands (Figure 11).

Table 2: General information about sampled transects investigated in December 2013 in the NNR Praděd (mean values ± standard deviation),* total sum of standing and lying deadwood

Age class	Young	Mature	Old
Altitude [m a.s.l.]	1080-1120	1160-1190	1150-1180
Exposition	Southern	Northern	Southern
Slope [%]	54	36	25
No. *Picea abies* [N/ha]	1515 ± 28	658 ± 46	205 ± 7
Standing Volume [m^3/ha]	450 ±16	246 ± 39	620 ± 107
Dead Volume [m^3/ha]*	39 ± 4	26 ± 10	110 ± 22
Ba [m^2/ha]	58 ± 2	35 ± 5	52 ± 5
Age	49 ± 12	115 ± 16	141 ± 40
Dbh [cm]	20 ± 6	24 ± 8	52 ± 23
Height [m]	17 ± 3	16 ± 4	25 ± 7
Vitality [1-5]	3 ± 1.2	2.5 ± 1.1	1.9 ± 0.9
Crown ratio [%]	44 ± 16	55 ± 18	64 ± 15
Slenderness ratio [h/dbh]	0.85±0.14	0.66±0.14	0.47±0.1
Distance to nearest neighbour [m]	1.4 ± 0.7	2.4 ± 1.3	4.2 ± 2.2

In total 951 trees were recorded, where of 606 were in the young age class, 263 in the mature class and 82 in old age class. The diameter distribution of the trees within the young stands is very similar to the mature stands, having most trees between 16 and 25 cm of dbh. In the old forest stage trees are relative evenly distributed over diameter classes (Figure 12).

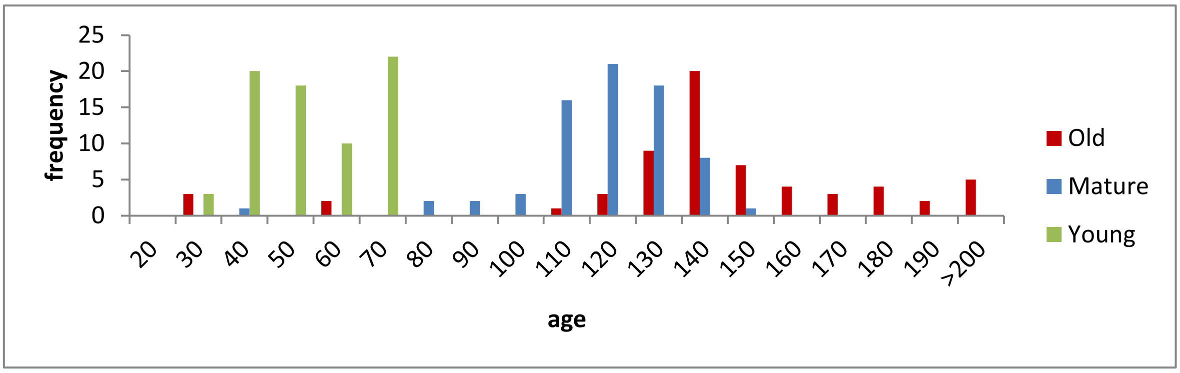


Figure 11: Age distribution of three different age classes sampled in NNR Praděd

The mean standing volume of living trees was calculated for the three age classes young, mature, old with 450 ± 16 m^3/ha, 246 ± 39 m^3/ha and 620 ± 107 m^3/ha. The average stem number is decreasing with age (1515 ± 28, 658 ± 46, 205 ± 7) and the basal area is highest in the young class (58±2, 35±5, 52±5).

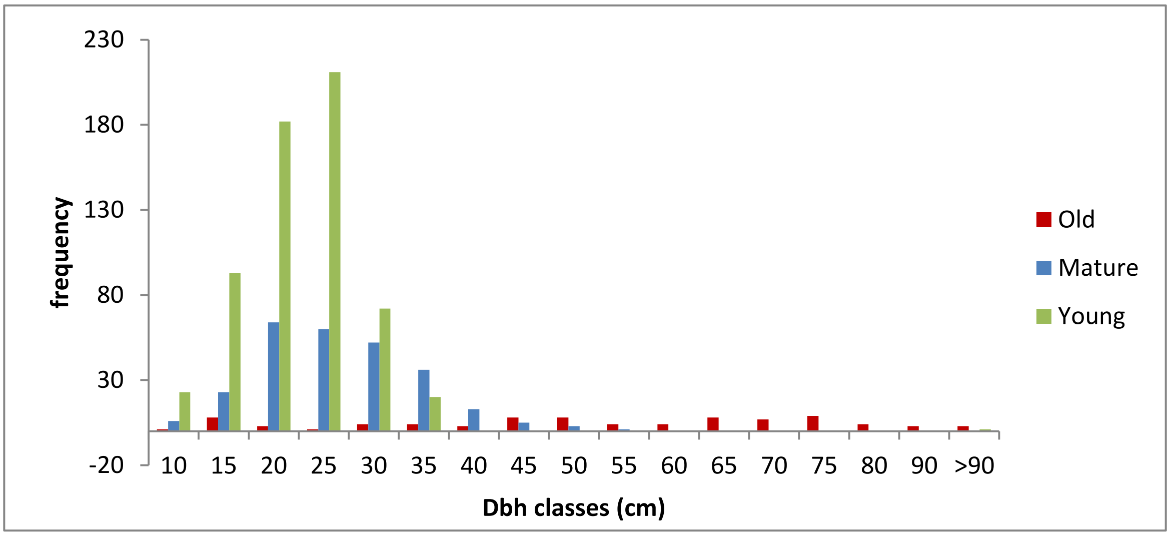


Figure 12: Dbh distribution of three different age classes sampled in NNR Praděd

Standing and downed deadwood were present in each of 6 study transects. On average 39 ± 4 m^3/ha were observed in young stands, 24 ± 8 in mature and 110 ± 22 in old stands (see Figures of respective transects in Appendix 19-24).

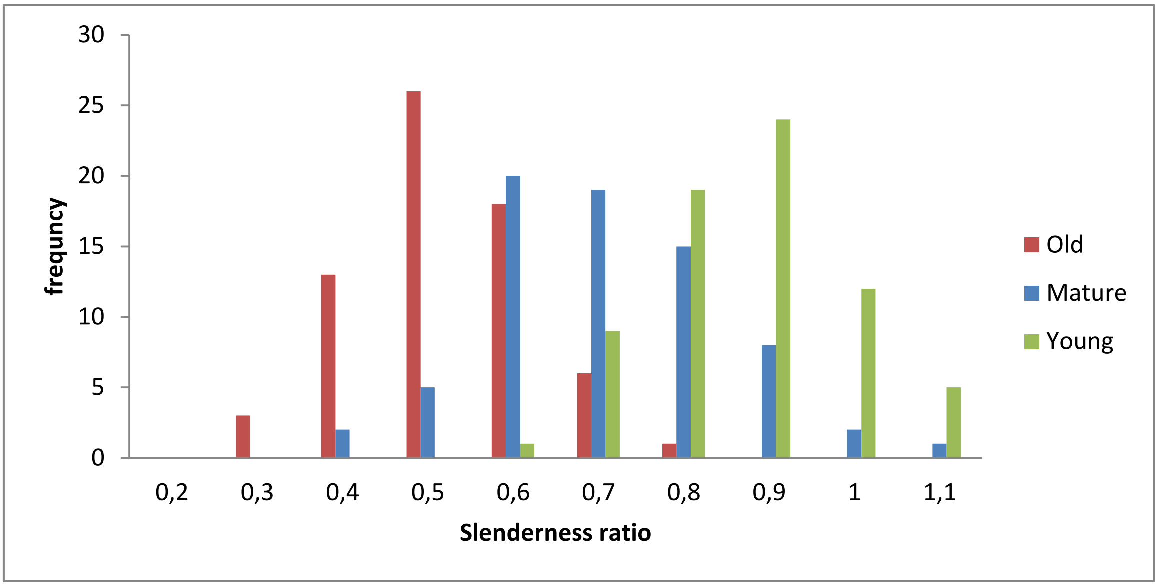


Figure 13: Height to dbh ratio showing potential vulnerability of the three investigated stands to wind storm

From Figure 13 it can be seen that the slenderness differs with age class. Old stands grow with a very low ratio between height and diameter and can thus be assumed to have high individual stability. For some of the individuals the H/D ratio approaches that of open-grown trees. Mature stands with its mean value of 0.66±0.14 conform to “stable” definition of REF, while young transects tend to be characterized as “unstable”, with a mean value of 0.85±0.14. The scatterings of respective age classes are shown in Figure 13.

4.2. Identification of growth response to wind disturbance

In the young stands 22 trees were randomly chosen from all three subsectors of the transect and cored twice from opposite directions. Both directions showed a similar growth trend (Figure 14). There is no significant difference between samples taken from regular and opposite direction (p= 0.83).

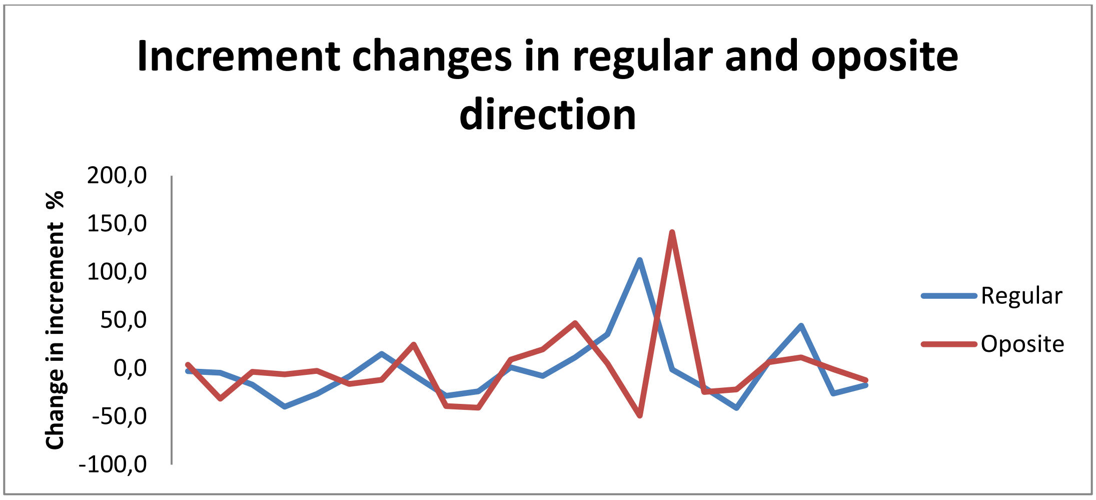


Figure 14: Comparison the mean growth trends of individuals cored from regular and opposite directions in Young stand. Blue values are cores taken from the regular side and the red curve represent cores from the opposite side of the tree N=22

Subsequently, all sampled trees (n=211) were tested against the null hypothesis of now growth response to wind disturbance in order to identify whether there is a release effect or growth depression. Over all trees there was a significant increase in growth by +6.7% (p= 0.004) (Table 3). However, the standard deviation of ±33.8 shows relatively high variation between samples.

Table 3: T-test for the Null hypothesis of no change in increment before / after the storm. N= 211

	Mean effect (%)	St. Dev	N	st. Error	t	p
All 211 trees	+6.7	33.8	211	2.3	2.9	0.004

Results thus support the hypothesis that the creation of an edge increases resource availability which, in turn promotes overall tree growth. Hence the alternative hypothesis that the residual tree population decreases in growth due to mechanical damage to branches, roots and xylem tissues could be rejected.

One of the specific objectives was to analyse growth responses to wind disturbance in different age classes (young, mature, old). All three age classes show a tendency to grow better after the storm event in the year 2004, although results were not significant results for two out of the three age classes. The old stands perform significantly better after the storm, whereas the young stands tend to be affected only marginally. The mature stand shows percentage moderate yet not significant increase in growth (Table 4).

Table 4: T-tests of the Null hypothesis of no change in increment before / after storm for three different age classes.

Age class	Mean effect (%)	st. Dev	N	st. Error	t	p
Old	+15.05	39.50	67	4.83	66	0.003
Mature	+5.39	31.94	72	3.76	71	0.157
Young	+0.38	28.20	72	3.30	71	0.908

4.2.1. Development stage

Correlation coefficients between parameters in this group were found to be strong (over 0.5) (Table 5). From an initial explanatory analysis it was not clear which parameter was best suited for the analysis. Each parameter from this group was therefore plotted against the change of increment in 5 years after windstorm relative to the 5 years before in order to check for the influence of each variable. (For more information see appendix – Fig 25-27). Neither dbh nor height proved to be correlated with increment response. The age has highest (Pcc) Pearson´s correlation coefficient (0.15) and proved to be correlated with increment response (p=0.03). Hence age was chosen as variable describing the development stage of an individual.

Table 5: Correlation of parameters in the development stage group (dbh, height and age)
N= 211, Red labelled correlations are significant at the level p <0.05 - Pearson

	Dbh	Height	Age
Dbh	1	0.86	0.70
Height	0.86	1	0.60
Age	0.70	0.60	1

Table 6: Correlation matrix of all parameters. Red values indicate significant correlations at p <0.05, N=211

	Dbh	Vitality	Distance	Distance to nearest neighbour	Bal	Height	Crown length	R.d. dbh	R.d. height	Age	5Y Increment	Ba
Dbh	1,0000	-,5350	,0252	,6262	,7163	,8611	,3727	,7523	,4763	,7036	,1136	,9717
	p= ---	p=,000	p=,716	p=0,00	p=0,00	p=0,00	p=,000	p=0,00	p=,000	p=0,00	p=,100	p=0,00
Vitality	-,5350	1,0000	,0115	-,4144	-,3491	-,5400	-,4604	-,5472	-,4166	-,3855	,0173	-,4527
	p=,000	p= ---	p=,868	p=,000	p=,000	p=,000	p=,000	p=,000	p=,000	p=,000	p=,802	p=,000
Distance to edge	,0252	,0115	1,0000	,0026	,0165	-,0305	,0600	,0155	-,0247	,0867	-,1063	,0548
	p=,716	p=,868	p= ---	p=,969	p=,812	p=,660	p=,386	p=,823	p=,721	p=,210	p=,124	p=,429
Distance to nearest	,6262	-,4144	,0026	1,0000	,5313	,4984	,3710	,5134	,1603	,5439	,0441	,6034
neighbor	p=0,00	p=,000	p=,969	p= ---	p=,000	p=,000	p=,000	p=,000	p=,020	p=,000	p=,524	p=0,00
Bal	,7163	-,3491	,0165	,5313	1,0000	,6024	,3735	,3300	,0522	,5471	,1700	,6712
	p=0,00	p=,000	p=,812	p=,000	p= ---	p=0,00	p=,000	p=,000	p=,450	p=,000	p=,013	p=0,00
Height	,8611	-,5400	-,0305	,4984	,6024	1,0000	,1594	,5979	,7771	,6028	,1077	,7889
	p=0,00	p=,000	p=,660	p=,000	p=0,00	p= ---	p=,021	p=0,00	p=0,00	p=0,00	p=,119	p=0,00
Crown	,3727	-,4604	,0600	,3710	,3735	,1594	1,0000	,3644	-,1482	,2961	-,0303	,3414
length	p=,000	p=,000	p=,386	p=,000	p=,000	p=,021	p= ---	p=,000	p=,031	p=,000	p=,661	p=,000
R.d.	,7523	-,5472	,0155	,5134	,3300	,5979	,3644	1,0000	,4176	,7670	,0961	,6922
dbh	p=0,00	p=,000	p=,823	p=,000	p=,000	p=0,00	p=,000	p= ---	p=,000	p=0,00	p=,164	p=0,00
Volume	,9500	-,4400	,0657	,5876	,6591	,7932	,3194	,6592	,4285	,6241	,0862	,9919
	p=0,00	p=,000	p=,342	p=0,00	p=0,00	p=0,00	p=,000	p=0,00	p=,000	p=0,00	p=,213	p=0,00
Ba	,9717	-,4527	,0548	,6034	,6712	,7889	,3414	,6922	,4123	,6427	,0934	1,0000
	p=0,00	p=,000	p=,429	p=0,00	p=0,00	p=0,00	p=,000	p=0,00	p=,000	p=0,00	p=,176	p= ---
Age	,7036	-,3855	,0867	,5439	,5471	,6028	,2961	,7670	,2502	1,0000	,1516	,6427
	p=0,00	p=,000	p=,210	p=,000	p=,000	p=0,00	p=,000	p=0,00	p=,000	p= ---	p=,028	p=0,00
R.d.height	,4763	-,4166	-,0247	,1603	,0522	,7771	-,1482	,4176	1,0000	,2502	,0096	,4123
	p=,000	p=,000	p=,721	p=,020	p=,450	p=0,00	p=,031	p=,000	p= ---	p=,000	p=,890	p=,000

4.2.2. Health

As parameters describing health of an individual tree vitality and crown length were recorded. The correlation coefficient of both parameters was -0.46 which is according to definition “moderate” relationship. Also in the Correlation matrix (Table 6) similar value of Pcc of both parameters can be seen. Thereafter both variables were plotted against the increment response in the respective age classes. Only in young stands there was a trend of growth response with tree vitality (Figure 15). There was a tendency of less vigorous individuals to respond stronger positive to wind disturbance. Vitality has also higher Pcc (0.33) but its significance was not proved (p = 0.11). Hence the vitality parameter was chosen as variable describing the health.

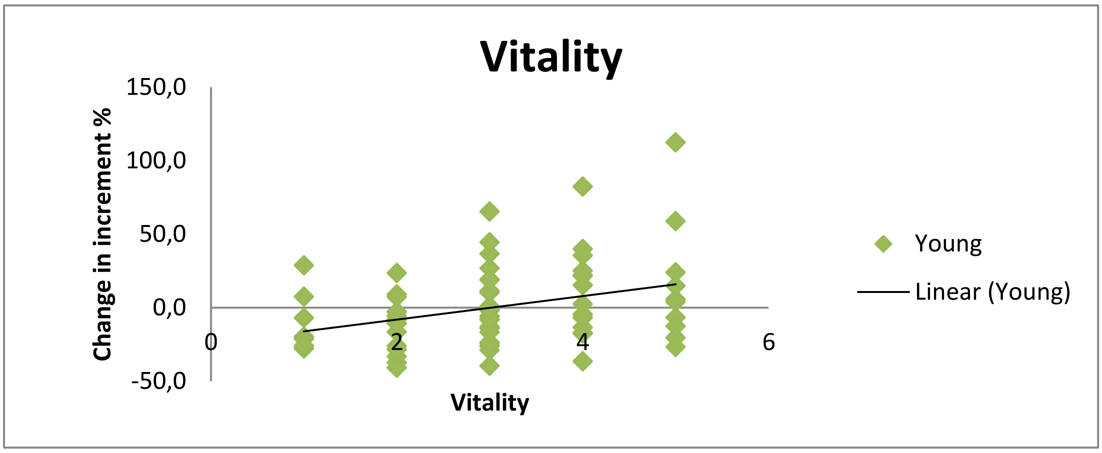


Figure 15: Relation of vitality in young stands to change in increment. 1- Excelent vitality N=144, Individuals with worse vitality have higher increments after windstorm in 2004

4.2.3. Competition

Many variables describing competition between species within the stand were considered in this study. In the field the following values were measured: bal, r. d. dbh, r. d. height, distance to the nearest neighbour and basal area. Correlation coefficients between parameters in this group were very diverse ranging from weak to strong (Table 7). Highest correlation was found between basal area and others parameters. On the other side the smallest was found in the case of R.d. height.

Table 7: Correlation of parameters in the Competition group (distance to the nearest neighbour, bal, r.d.dbh, r.d.height, ba) N= 211, Red labelled correlations are significant at the level p <0.05 – Pearson

	Distance to the nearest neighbour	Bal	R.d.dbh	R.d.height	Ba
Distance to the nearest neighbour	1.0	0.53	0.51	0.16	0.60
Bal	0.53	1.0	0.33	0.05	0.67
R.d.dbh	0.51	0.33	1.0	0.42	0.69
R.d.height	0.16	0.05	0.42	1.0	0.41
Ba	0.60	0.67	0.69	0.41	1.0

All parameters were also plotted against increment response and then checked for potential correlation. Both relative dimensions and distance to the nearest neighbour were excluded due to the absence of any kind of association with growth change (for more details see respective figures in the Appendix). Whereas the bal and ba show some relationship to growth changes in young stands (Figure 16), no relationship was found for mature (Pcc: 0.1; p = 0.5) and old stands (Pcc: 0.22; p = 0.34). The sampled trees in younger development stages tend to show a decrease in increment response after storm with increasing ba, while trees with a bigger bal showed a tendency to grow slightly better (Fig 16), meaning that individuals under higher competitive pressure tend to respond with higher increments to wind. Bal was selected as the variable representing competition within the final multiple regression model, based also on the strongest correlation to increment response (Table 6).

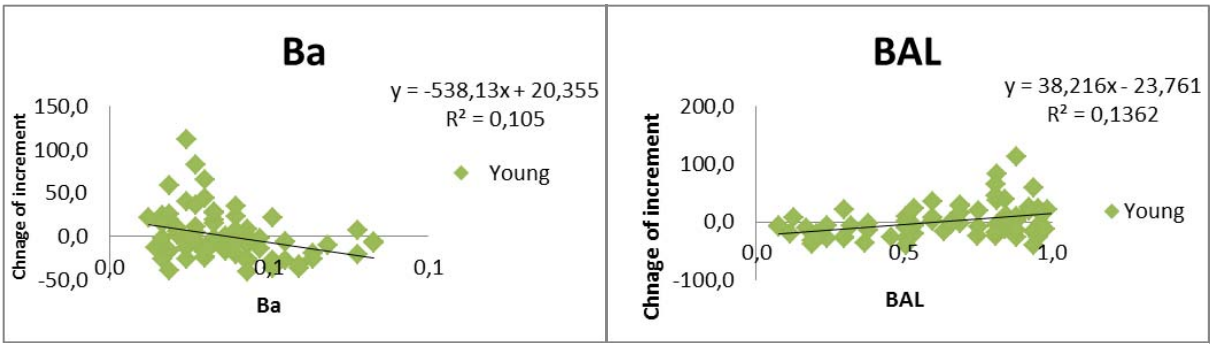
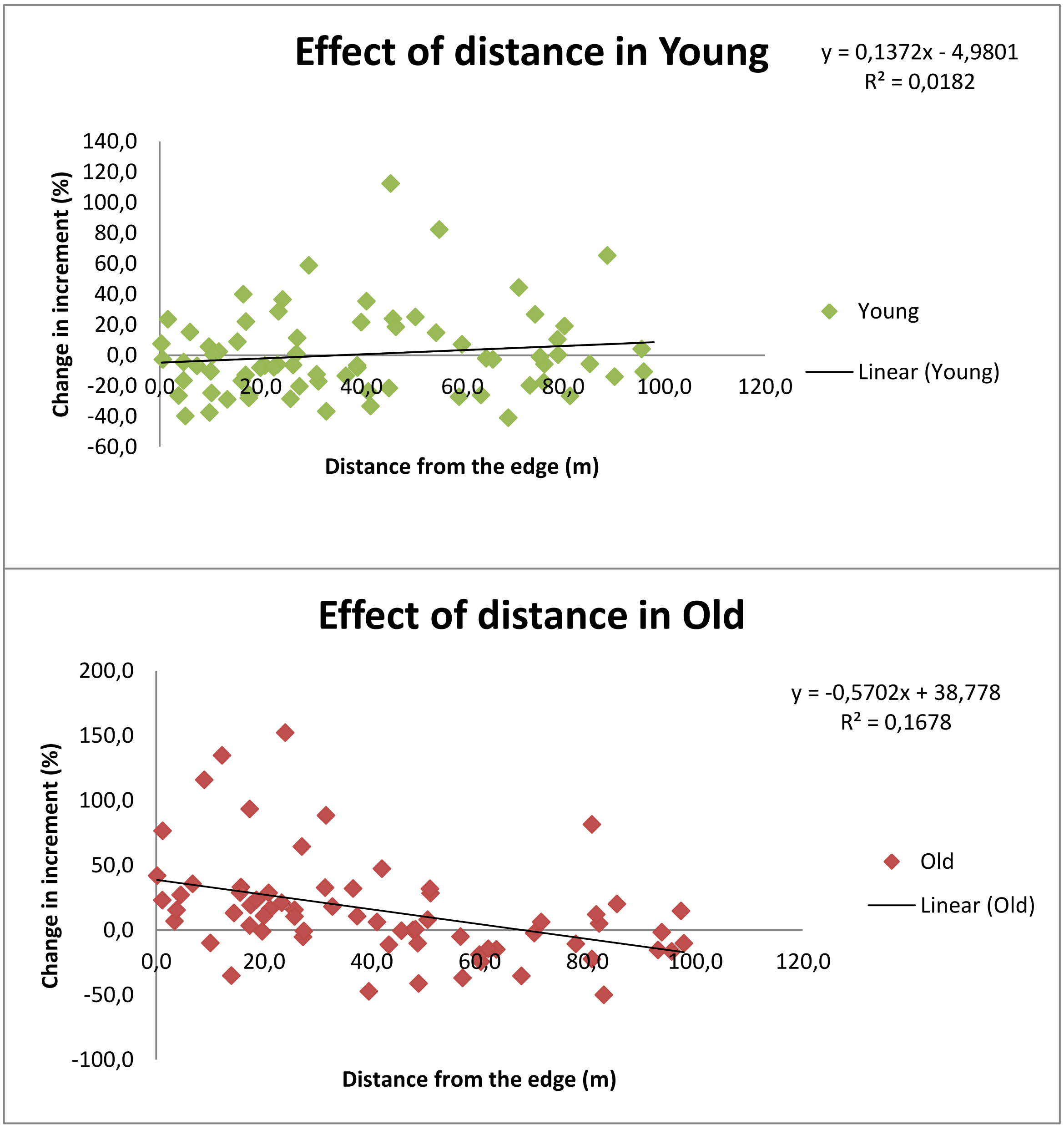


Figure 16: Basal area, basal area of larger trees (Bal) and their relationship to increment change in after wind disturbance in young stands.

4.2.4. Distance

The fourth group of potential explanatory variables consisted of only one parameter - distance to the edge of the windthrown area.

The role of distance from the edge of the disturbed area for the three different age classes is shown in Figure 17. Apart from the old stands, distance from the windthrow edge does not influence the increment response of the surviving trees. Each of two sectors was tested separately in order to determine, what role played distance in growth response (Table 8).



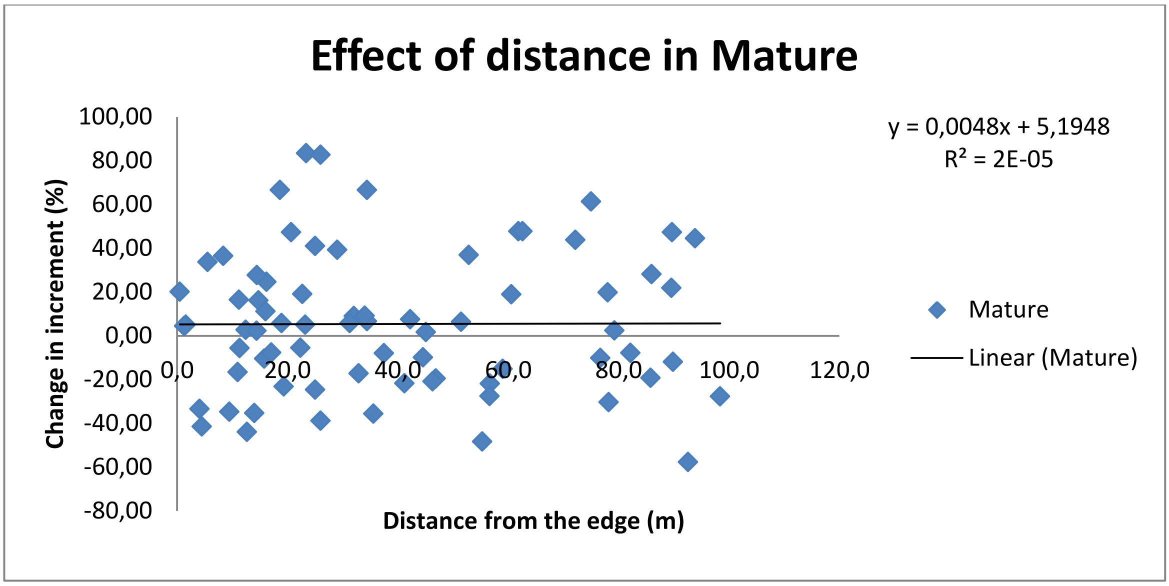


Figure 17: The effect of distance from the edge on increment response to disturbance within the three different age classes in NNR Praděd.

In the first 50 m, an increase in increment response was observed in all transects except for the young stand. However, these responses were significant only for the old stands. The second 50m vary more widely between the age classes. Whereas mature stands show a similar increase in the increment response as in the first 50m, the young stands turn from a decrease in increment to a small increase in response. The old stands also invert their growth response but to negative values. Even so none of these results for the second transect sectors were statistically significant (Table 8.).

Table 8: The role of distance from the edge of windthrown for explaining the release effect (t-test) for the first 50m and second 50m of three different age classes. $p < 0.05$

Age class	Mean	st. Dev	N	st. Error	t	p
Old I. sector	+26.38	41.24	41	6.44	4.09	0.000
Old II. sector	-4.82	27.96	25	5.59	-0.86	0.402
Mature I. sector	+5.01	31.28	48	4.51	1.11	0.272
Mature II. sector	+6.15	33.91	24	6.92	0.89	0.381
Young I. sector	-1.42	27.84	49	3.96	-0.38	0.724
Young II. sector	+4.06	29.20	24	5.96	0.68	0.504

4.2.4.1. The interaction between distance and the other explanatory variables

The release effect was found only in the first 50m in the Old stands (Table 8). The first 50m were compared with the second 50m and selected variables were tested to identify interaction effects between them (age, vitality, bal). In the old classes, out of the tested variables, chosen for regression analysis, only bal differs significantly in the first 50m compared to the second 50m (Table 9). Other variables in old stands did not show any

Table 9: Comparison of age, vitality and Bal within first and second sector of old stands, p <0.05, N=67

Old class	Mean	st. Dev	N	st. Error	t	p
Age / Age II	134.5 / 143	30.87 / 55. 14	24	60.72	-0.70	0.488
Vitality / Vitality II	1.64 / 1.88	0.86 / 0.83	24	1.05	-1.14	0.19
Bal/ Bal II	83.52 / 72.85	12.59 / 16.86	24	21.77	2.45	0.022

significant difference at a confidence level of 95%. In the mature age classes no significant differences within the sectors were found in the analysed variables (Table 10).

Table 10 : Comparison of age, vitality and Bal within first and second sector of mature stands, p <0.05, N=72

Mature class	Mean	st. Dev	N	st. Error	t	p
Age / Age II	120 / 112	11,31 / 22,15	24	25,78	1,54	0,136
Vitality / Vitality II	2,75 / 2,38	1,29 / 0,97	24	1,47	1,25	0,224
Bal/ Bal II	0,64 / 0,59	0,27 / 0,25	24	0,32	0,82	0,419

Young stands have expressed significant difference in age (Table 11), particularly trees in the first 50m seem to be younger (43±10.71) than in the second part (62±5.59). Other variables did not show any significant differences at a confidence level of 95%.

Table 11: Comparison of age, vitality and Bal within first and second sector of young stands, p <0.05, N=72

Young class	Mean	st. Dev	N	st. Error	t	p
Age / Age II	43.3 / 62.1	10.71 / 5.59	24	11.2	-8.2	0.000
Vitality / Vitality II	2.92 / 2.92	1.35 / 1.18	24	1.91	0.00	1.000
Bal / Bal II	0.57 / 0.66	0.28 / 0.26	24	0.33	-1.27	0.216

4.3. Multiple linear regression analysis

Based on this individual factor analysis age, vitality, bal and distance to the edge were selected as parameters representing the four dimensions: development stage, health, competition and distance in the multiple linear regression.

In the individual factor analysis, the growth response of old stands changed significantly with distance, with each meter of distance from the edge experiencing a 0.6% reduction (Figure 17). In addition to the distance the intercept was also significant (0,000). Overall there was a significant positive growth response of +38.8% at the edge of the stand (i.e. when distance =0) and this positive growth response is decreased by -0.6% for every meter from the edge (Table 12). So, statistically, there was a release effect for the first 68 m, and after that, in the remaining 32 m of the transect the growth response was negative (Fig. 14).

Bal and age were also found to be negatively associated with increment. In contrast vitality was positively associated with growth response. In the multiple linear regression framework, however, only distance and the intercept were retained as statistically significant at p = <0.05 in a backwards selection (Table 12).

Table 12: Output from MLR for old stands. Distance proved to be significant driver of increment response. N = 67, p <0.05

Old class	Coefficients	Standard Error	R^2	P-value
Intercept	38.346	25.921	0.176	0.144
Bal	-5.047	18.736		0.786
Distance	-0.582	0.161		0.001
Vitality	3.866	5.193		0.459
Age	-0,021	0.122		0.862
Intercept	34.595	14.434	0.175	0.019
Bal	-3.872	17.353		0.824
Distance	-0.583	0.160		0.001
Vitality	3.864	5.153		0.456
Intercept	32.699	11.580	0.174	0.006
Distance	-0.582	0.159		0.001
Vitality	3.501	4.853		0.473
Intercept	38.778	7.914	0.168	6.69E-06
Distance	-0.570	0.157		0.001

The final model explained 16.8% of the variation in increment response in the old transects.

The intercept of the MLR for the mature stands is not significant, meaning that there is no significant effect of the wind disturbance on growth response in the mature stands overall (Table 13.). Moreover also the individual factors do not have an influence on how the stand reacts to wind disturbance.

Table 13: Output from MLR for mature stands. None of predictors proved to be significant driver of increment change. N = 72, p <0.05

Mature class	Coefficients	Standard Error	R^2	P-value
Intercept	-34.479	37.321	0.035	0.359
Vitality	-0.294	4.923		0.953
Bal	-1.980	21.713		0.928
Distance (m)	0.037	0.138		0.788
Age	0.351	0.271		0.199
Intercept	-34.318	36.950	0.035	0.356
Bal	-2.888	15.353		0.851
Distance (m)	0.037	0.137		0.786
Age	0.348	0.264		0.192
Intercept	-38.645	28.718	0.034	0.183
Distance (m)	0.039	0.135		0.773
Age	0.370	0.236		0.122
Intercept	-35.826	26.840	0.033	0.186
Age	0.359	0.232		0.125

There is no significant growth response with increasing distance from the edge in young stands either (Figure 15). Also age did not influence growth changes of individuals significantly. Bal was the second most influential variable in the backwards selection, but not significant at p=0.05. Vitality as a parameter describing the health status of the tree population was significantly negatively related to growth response. In addition to vitality the intercept was also significant at p=0.007. Overall the vital trees suffer on average a 16.4% growth loss (-24.4 at vitality=0 + 8.0 for the first vitality class), and only vitality classes 4 and 5 report (on average) a positive growth response to wind (Table 14). However, vitality only explained 11.5% of the variation in increment response in the young stands.

Table 14: Output from MLR for young stands. Vitality proved to be the single significant driver of increment change. N = 72

Young class	Coefficients	Standart Error	R^2	P-value
Intercept	-42.458	22.198	0.155	0.0606
Vitality	5.610	3.389		0.103
Bal	21.220	14.977		0.161
Age	0.241	0.490		0.624
Distance	0.006	0.220		0.980
Intercept	-42.834	16.484	0.155	0.011
Vitality	5.624	3.316		0.094
Bal	21.267	14.751		0.154
Age	0.251	0.258		0.332
Intercept	-29.543	9.290	0.143	0.002
Vitality	5.102	3.271		0.123
Bal	22.168	14.717		0.137
Intercept	-24.396	8.717	0.115	0.007
Vitality	8.024	2.659		0.004

5. Discussion

5.1. Discussion in the context of hypotheses and previous findings

The analysis of functional impacts of disturbances on forests have received often only limited scientific attention in the literature to date. In addition, these effects are currently neglected in the monitoring and assessment of the economic damages of e.g. wind events, as these assessments are entirely focused on structural damages (Nieuwenhuis and O'Connor 2001; Schelhaas et al. 2003).

The main hypotheses tested in this thesis were whether the release from competitors will promote growth after wind disturbance due to the availability of additional light and nutrients, or if due to the mechanical damage to branches, roots and xylem tissues tree growth will decrease.

In previous studies, negative growth responses have been reported at the landscape scale, e.g., for Norway spruce after storm Gudrun (Seidl and Blennow 2012), whereas at the level of individual trees not only negative but also positive wind-induced growth responses have been observed (Ueda and Shibata 2004; Zielonka and Malcher 2009; Hadley and Knapp 2011). In this study an overall positive growth response of trees after storm at the stand level was found.

My results support the first hypothesis on increased growth after wind disturbance particularly for old stands. Generally the strongest growth response to increased resource availability is expected in younger development stages, where the competition for light, water and nutrients is much higher (Perry 1985; Kocher and Harris 2007). Notwithstanding the conventional assumptions in forestry, even old trees can respond strongly to the availability of more resources and continue growing despite their advanced age (Latham and Tappeiner 2002).

One possible reason for the significant positive growth response of the old and not the mature or young stands might be the fact that they were overall healthier (mean value of vitality 1.9 compared to 3 in Young and 2.5 in Mature stands). Larcher (2001) described vitality as a crucial factor for surviving the effect of stress, i.e. as capacity to live, grow, develop, to resist the stress and to adapt to changing environmental conditions. It is thus possible that the higher vitality in old stands resulted in an improved capacity to exploit the additional resources and turn them into higher increments.

In the young stands an opposite relationship was found. Contrary the young stands despite their high competitive conditions seem to be affected only marginally. The only measurable release effect was detected in trees “4 and 5” in this context having a low vitality class. Lapointe et al (2006) found that the growth response of spruce is limited by the most limiting resource, whether it is soil nutrients or light. The studied young stands were typically characterized as homogeneous even-aged. In this regard, it can be therefore assumed that the most limiting factor in this case might have been supplemented. Probably additional resources (water, nutrients) helped to the suppressed trees to compensate slightly for their social position. Although, out of the gathered information, it could not be found which resources were added. Another reason for such reaction may have been the fact that trees with low vitality class have mostly also worse social position. That might have resulted in lower mechanical damages caused by the windstorm to the branches, roots and xylem tissues (Nielsen and Knudsen 2004) especially due to their “sheltered” positions in the forest stand. However, there may be intrinsic growth limitations in these young trees in addition to other factors like site, tree characteristics or both that was not measured but still could have an influence on growth response (Ueda and Shibata 2004).

No significant release or depression effect was found on growth response in the mature stands. Overall trees in mature transects tend to have 5.4% higher increments compared to years before the storm, but not statistically significant.

In the old stand it was also found this positive growth response related with distance. It means there was a release effect for the first 68 m, and after that, in the remaining 32 m of the transect the growth response was negative. Others age classes didn´t shown a significant relationship between distance and growth response. The edge effect in forest ecosystems differs considerably between studies and with the respective indicators analysed. While in the case of biodiversity there might be effects for distances of 100 m to 1 km along the edge-to-interior gradient (Broadbent et al. 2008; Bueno et al. 2012), the growth response is considerably more local and typically relate to distances between 5 and 50 m (Oosterhorn and Kappelle 2000; Powell and Lindquist 2011). Generally, the edge effect is strongest at the boundary from 0 to 20 m, e.g., with regard to the number of understory plants (Euskirchen et al. 2001), tree density (Russell et al. 2000; Oosterhorn and Kappelle 2000; Harper and Mac-Donald 2001; Cayuela et al. 2009) and stem and crown shape (Oliver and Larson 1996; Matlack and Litvaitis 1999). Moreover, the extent of the forest edge effect is modified by the characteristics of the adjacent ecosystem (Burley et al. 2010) as well as by the length of time over which the edge exists (Lopez et al. 2006). Statistically validated 68m in this study underlines the assumption about importance of such a distance dependent phenome for the wider area of the NNR Praded.

Individual growth response and formation of forest are influenced by many factors. In this study several were considered: development stage, health, competition and also already mentioned distance as other factor. Nevertheless there are also several factors like, climate variation, genetic predisposition, microsite condition, degree of anthropogenic load, and other which were not considered in this study but could also have an influence on growth response.

All three age classes varied not only in growth response but also in inciting factors of growth response to wind event in the year 2004. While the old stands reported increase in productivity related to distance to the edge with windthrow, young stands showed increased productivity only by individuals with bad vitality and finally mature stands demonstrated none significant response at all.

The controlling the majority of components contributing to change is an intricate task, for which several different approaches have been described, resulting in various final results. In the retrospective disturbance studies the coniferous forests stands differ conclusively in response. Hereby might be then of interest to take into account both options - suppression and release.

5.2. Forest structure

Notwithstanding the fact that relatively homogeneous stands of mountain Norway spruce were selected for investigation, there are some factors that require a further discussion. Transects differ not only in age, which was a prerequisite for the selection and a design variable of the analysis, but also in their exposition and slope. While the young and old stands are south exposed with slopes 54% and 25% respectively, the mature stands have a northern exposition and a slope of 36%. Transects were established by following the contour lines to minimize effects of different wind exposure within a transect. Interesting point may have been fact the trees from the mature class 115 years old (mean value from Table 2.) are smaller (16m) in term of height than the 49 years old trees (mean value Table 2.) from young stands (17). This would indicate that these are two different site types despite to the previous selection for resemblance.

Although the sites differ in age, exposition and slope, plots have the same management history of minimal intervention, mimicking “close to nature” conditions. Thus it was assumed that differences in management and management history did not affect the analysis.

Čada and Svoboda (2011) previously conducted dendrochronological research in the NNR Praděd. Comparing their stand characteristics with the old stand selected for this study, close similarities except of height and standing volume can be observed (Table 13). This underlines that in every way the selected old stands are representative for the wider area of the NNR Praded.

Table 15: Comparison of basic characteristics of old growth stands in NNR Praděd from Čada, Svoboda (2011) and study plots.

	Čada and Svoboda (2011)- old stands	This study – old stands
No. Picea abies [$N^{/ha}$]	205	205
Standing Volume [$m^{3/ha}$]	371	620
Dead Volume [$m^{3/ha}$]	99	110
Ba [$m^{2/ha}$]	40	52
Dbh [cm]	48	52
Height [m]	19	25

5.3. Study design

As mentioned in the Material and Methods, the study design was a replication of 20*100m transects divided into two sectors. However, in the field the transects were divided into three sectors (20m, 30m, 50m) for easier data collection. During explanatory analysis it was decided to continue further with division into two sectors. Decision was performed in order to have to comparable areas in terms like size, basal area, number of individuals, competition etc. Although all trees in certain transect were measured in terms of position, no information has been obtained about trees standing outside of the study plots. This lack of data influenced the ability to correctly determine the distance to the nearest neighbour, and inhibited the use of spatially explicit competition indices. This methodological shortcoming is likely affecting especially old growth stands, as they have the lowest stocking density of all development stages.

In the field only position and dbh were measured of all threes. Other parameters like height, crown length, were recorded only for the trees randomly chosen for coring. As an additional health and competition-related parameter the crown diameter could be measured. Zhu et al. (2000) measured wind speeds and crown thickness within crown of Japanese black pines (Pinus thunbergii Parl.) and he highlighted that crown features can have a large influence on tree recovery after windstorm. Crown width is also used in calculating competition indices based on crown overlap (Biging and Dobbertin 1992; Sanchéz-Gonzáles et at. 2007).

It is well known that different soil types and their properties are an important factor in determining the rooting habit and stability of a tree. In order to certainly describe particular site conditions soil analysis would be desirable. It must be mentioned no soil samples were collected during the field work. Although Banaš et al. (2001) states that the soil type was classified as a modal podsol and moreover should be same for all age classes, because of the same geomorphological features (Čgs, 2015).

The sum of 212 trees was cored and 211 were used for analysis (one was too young). Generally, a higher number of trees would have helped to increase the discriminant power in the statistical analysis, which was found to be poor to moderate. However, the permission for coring trees was granted only to 212 individuals from the administration of NNR Praděd.

Trees were cored once from a fixed direction, which is also the wind direction. Additionally 22 samples were cored also from the opposite direction, to test for a potential effect on the growth response in relation to the coring direction. However, this test could only be done for the young stand, where coring was not limited by the administrative personal of NNR Praděd. It was decided to take cores in 1.3 m height (see Field methods) but the duration needed to reach this height is unknown, inducing uncertainty in determining the exact tree age. Regarding the fact that *Picea abies* regeneration can persist for decades in shade and therefore it is difficult to assess the year of germination (Niklasson 2002). The literature gives different information here e.g. exposition, slope, microsite, competition and other factors might influence the regeneration time. Čada

(2011) did some research in NNR Praděd on old growth stands and cored trees in 0.5 m of height (Figure 18.). According to the fact that the highest age frequency of individuals was around 190years and in this study the old stands were 140, current age might have been underestimated.

A further limiting factor of the analysis was the relatively short time series available for analysis. The analysis of a longer time series would be desirable to test also for long-term effects of disturbances on tree growth.

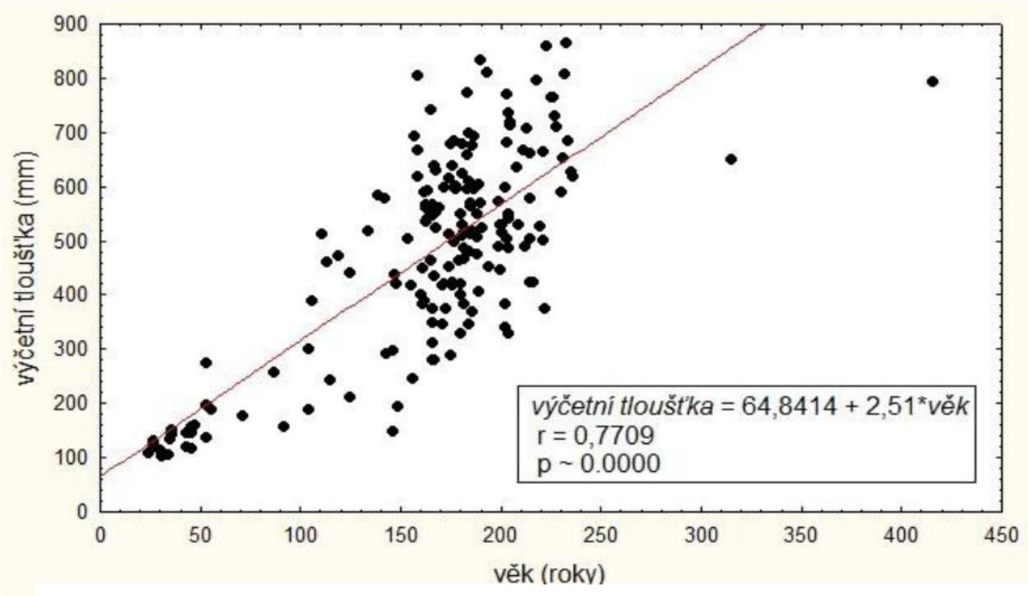


Figure 18: Age distribution according Čada in NNR Praděd in 2011. Investigation focused on old stands. y-axis units are "milimeters", x-axis units are years, The highest frequency of individuals can be found between 160 and 230 years

5.4. Methodological Issues

A prior reduction of correlated predictors in four variable groups was found to be an appropriate method to address the problem of multicollinearity in this study. The selected variables were analysed by means of the variance inflation factor, which confirmed that the requirements of Multiple linear regression were met through this a priori selection. However, again, the approach to eliminate variables in order to avoid multicollinearity is to some degree subjective. Also Morzuch and Ruark (1991) state that variable selection due to avoid multicollinearity reduces the overall explanatory power of the model and neglects the impact that these omitted variables might have on the response variable.

As an alternative, Principle component regression (PCR) helps to overcome the problem by orthogonalization of the predictors. However, also the elimination of principle components from the PCR is an intricate task, for which several different approaches have been described in the literature, resulting in various final PCR models. Ultimately, the choice of a variable selection routine is rather arbitrary also in the context of PCR (Jolliffe 2002).

Nevertheless there are also other methods for dealing with multicollinearity that could have been applied, such as the condition index (Hedderich and Sachs 2011).

Furthermore, taking climate variation into account explicitly (Seidl and Blennow 2012a) could have enhanced the results further. However, instead of calculating climate variation, problems were circumvented by averaging over several years pre and post disturbance, which is nowadays also common approach. For example Šplechtna et al. (2005) considered in their study in the Alps only the release effect in the interval 50-100% boundary line. Čada et al. (2011) calculated absolute growth changes for each year of each series (except for the first and last ten years) by subtracting the prior ten-year mean from the subsequent 10-year mean. In terms of estimating the release effect it can be assumed to be a useful approach of comparing values before and after storm. For this purpose in this study five year averages were used.

Tsvetanov et. al (2011) investigated the majority of survival trees at the border of a severe windstorm in Parangalitsa reserve and they found predominantly delayed release effect up to five years after the disturbance. This underlines the appropriate choice of the five years approach. Nevertheless there are also other methods commonly used for the detection of a release effect such “absolute increase, moving average” and many others, which might have been applied as well. Typically each technique has its own advantages and influences the results in particular ways (for more see Robino and McCarthy 2004).

6. Conclusion

Wind disturbances strongly shape forest structure, function and composition in European forests. Major hurricanes generate large but heterogeneous openings, increase coarse woody debris, create pit-and-mound microsite and change understory light availability. The overstorey exhibit a range of responses to wind events, including sudden or delayed mortality, reduced or enhanced growth, recovery, or sprouting.

However, the effects of disturbances on forest ecosystems in central Europe are still incompletely understood, despite the importance of these processes for forest management (e.g., for managing recent, large-scale, high-severity disturbances in the region).

Indeed, in recent decades several major storms have caused wide-spread damage in European mountain forests and have led to research focused on the influences of natural disturbances and the resilience of these forests to disturbances.

Less attention has been paid to the reaction of individual trees surviving windstorms. The heterogeneity of tree reactions to disturbance and subsequent developmental pathways are still relatively unknown. Moreover, one manifestation of climate change is likely to be an increase in the frequency and severity disturbances which further increases the importance of understanding the role of these natural disturbances in ecosystem dynamics.

Using a tree-ring approach, this work contributes to a better understanding of disturbance processes by investigating the growth reaction of different age classes of Norway spruce forests in the Czech Republic to a windstorm in 2004.

Because of variability in response over different age classes, it can be concluded that both release effects and growth depression after wind disturbance occur simultaneously. Future research should aim to better establish the context that discriminates between these two converse effects, and to quantify the overall net effect of wind disturbance on surviving tree populations at the landscape scale.

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Appendix

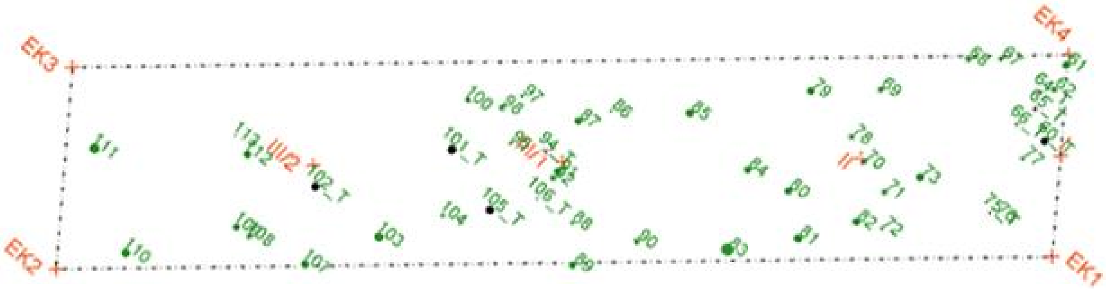

Figure 19: Spatial representation of trees in the transect no. 6 - old forest. Green dots are living trees and black dots with mark "_T" representing dead trees.

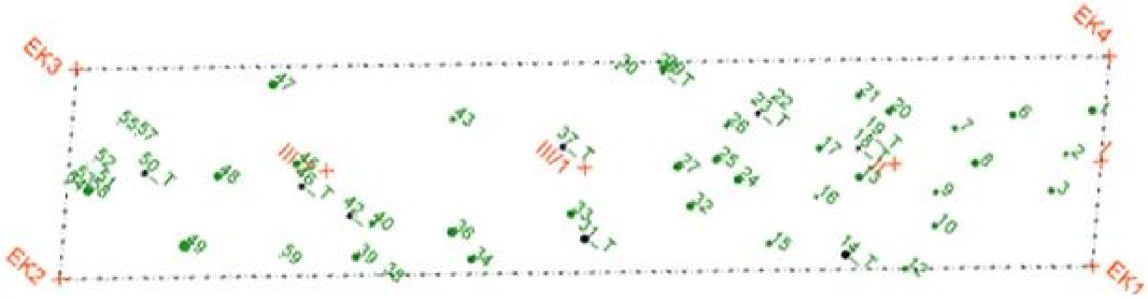

Figure 20: Spatial representation of trees in the transect no. 5 - old forest. Green dots are living trees and black dots with mark "_T" representing dead trees.

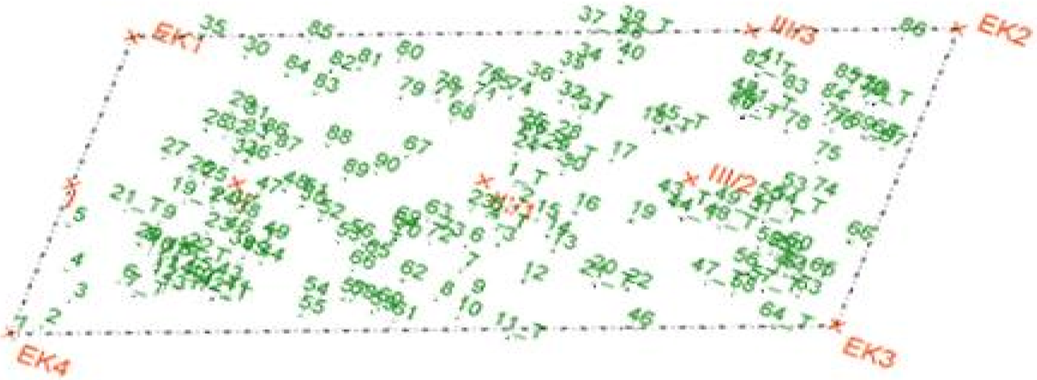

Figure 21: Spatial representation of trees in the transect no. 1 - Mature forest.
Green dots are living trees and black dots with mark "_T" representing dead trees.

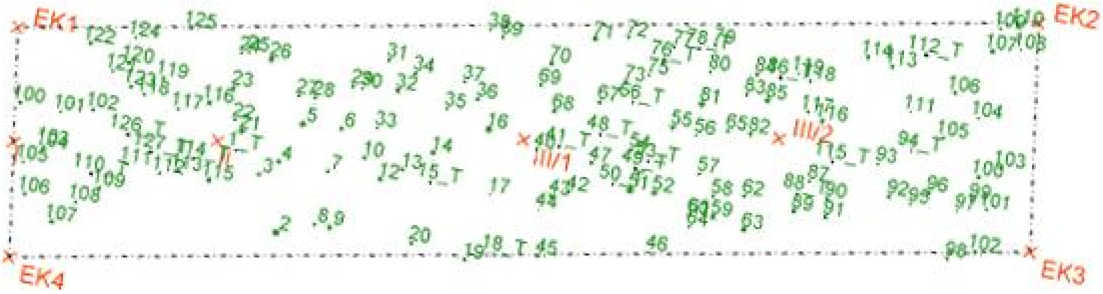

Figure 22: Spatial representation of trees in the transect no. 2 - Mature forest. Green dots are living trees and black dots with mark "_T" representing dead trees.

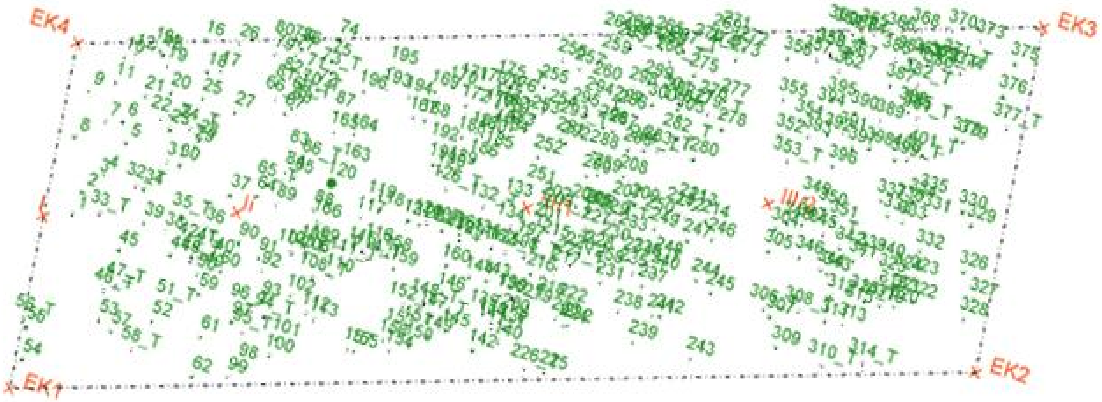

Figure 23: Spatial representation of trees in the transect no. 3 -Young forest. Green dots are living trees and black dots with mark "_T" representing dead trees.

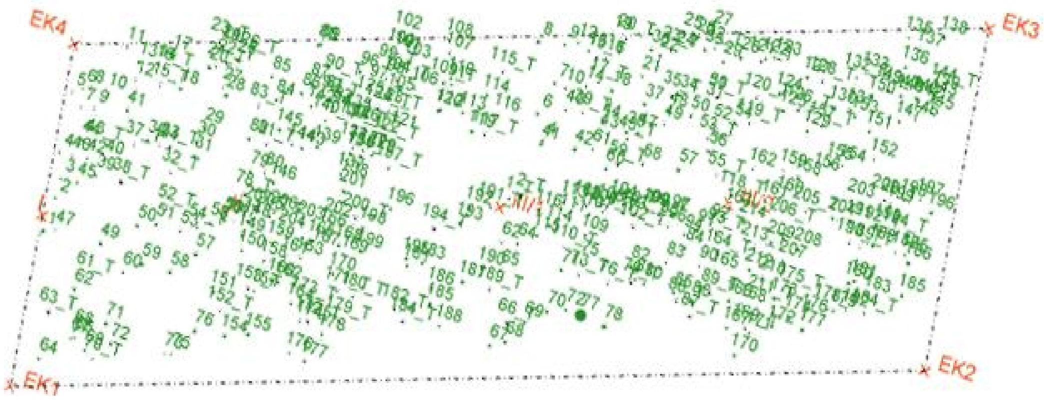

Figure 24: Spatial representation of trees in the transect no. 3 -Young forest. Green dots are living trees and black dots with mark "_T" representing dead trees.

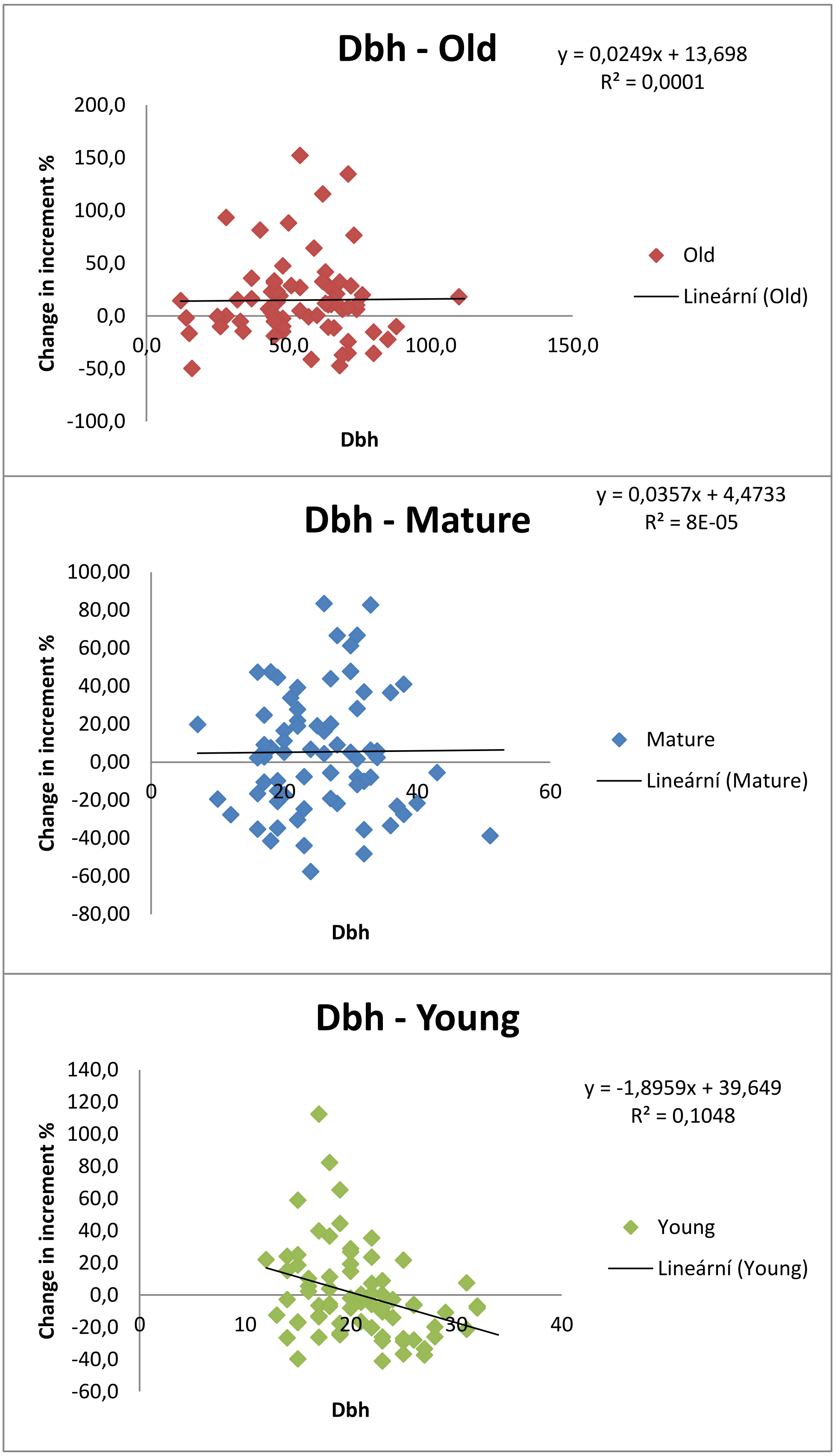

Figure 25: Relation between dbh and change in increment in three different age classes. (N=67, 72, 72)

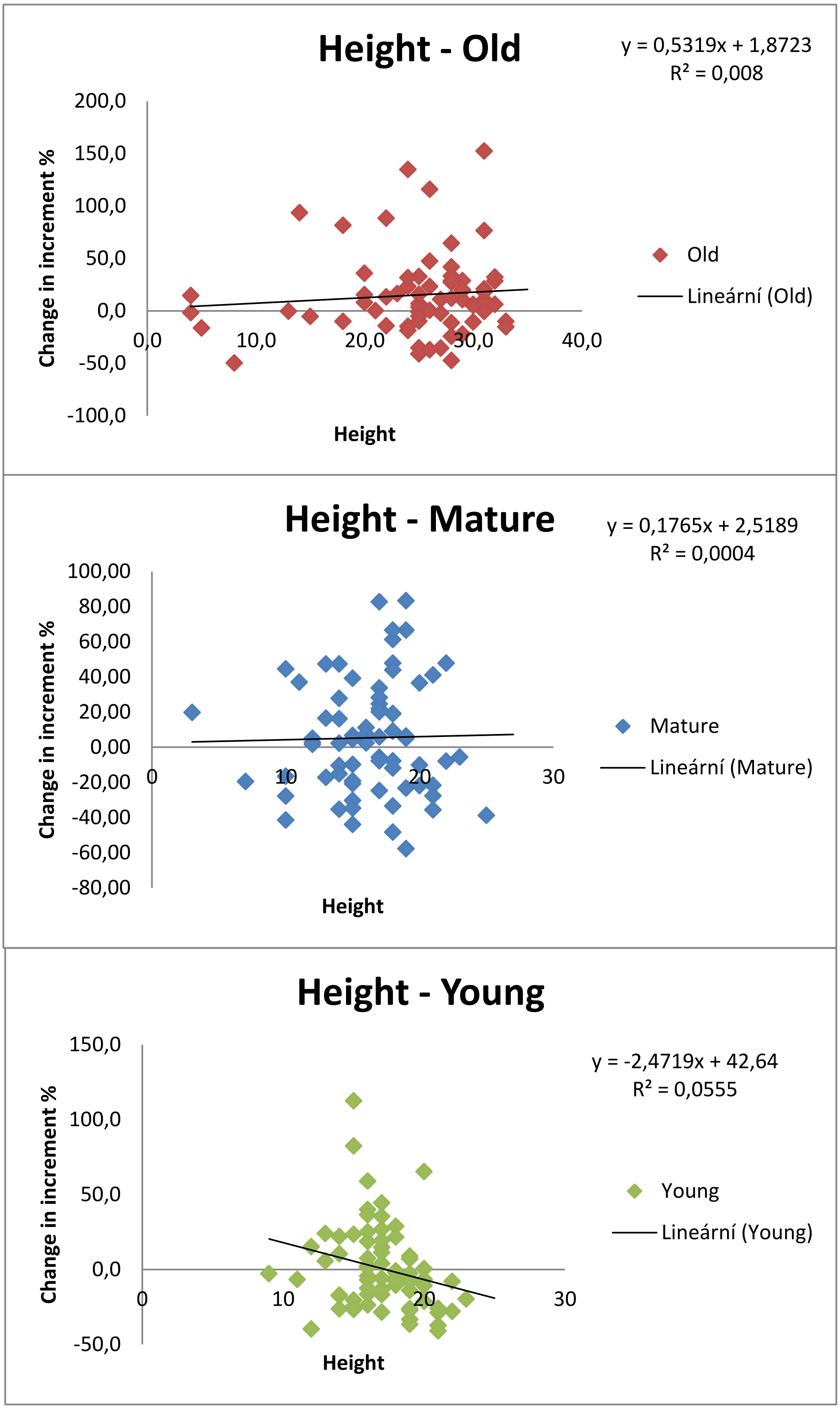

Figure 26: Relation between height and change in increment in three different age classes. (N=67, 72, 72)

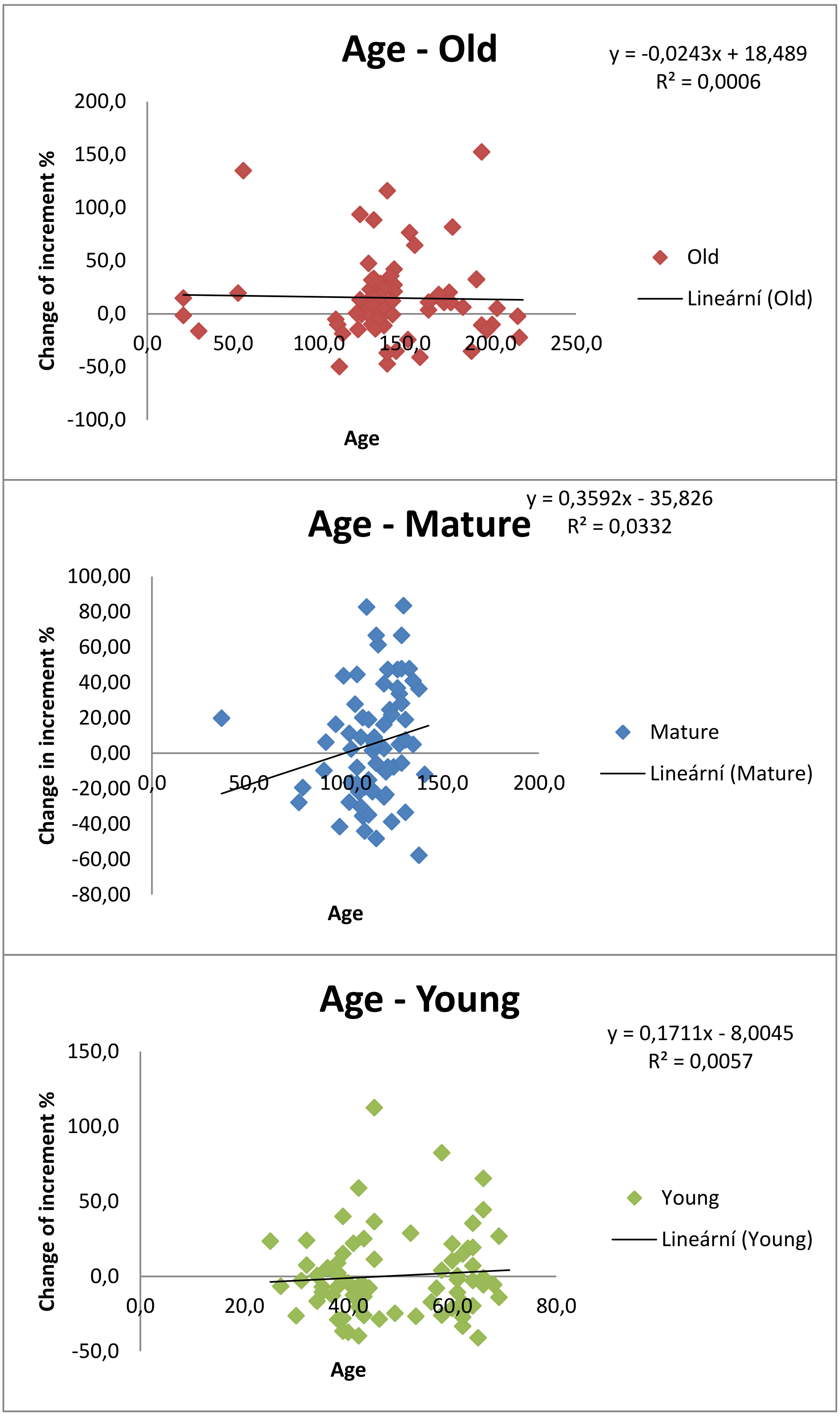

Figure 27: Relation between age and change in increment. in three different age classes. (N=67, 72, 72)

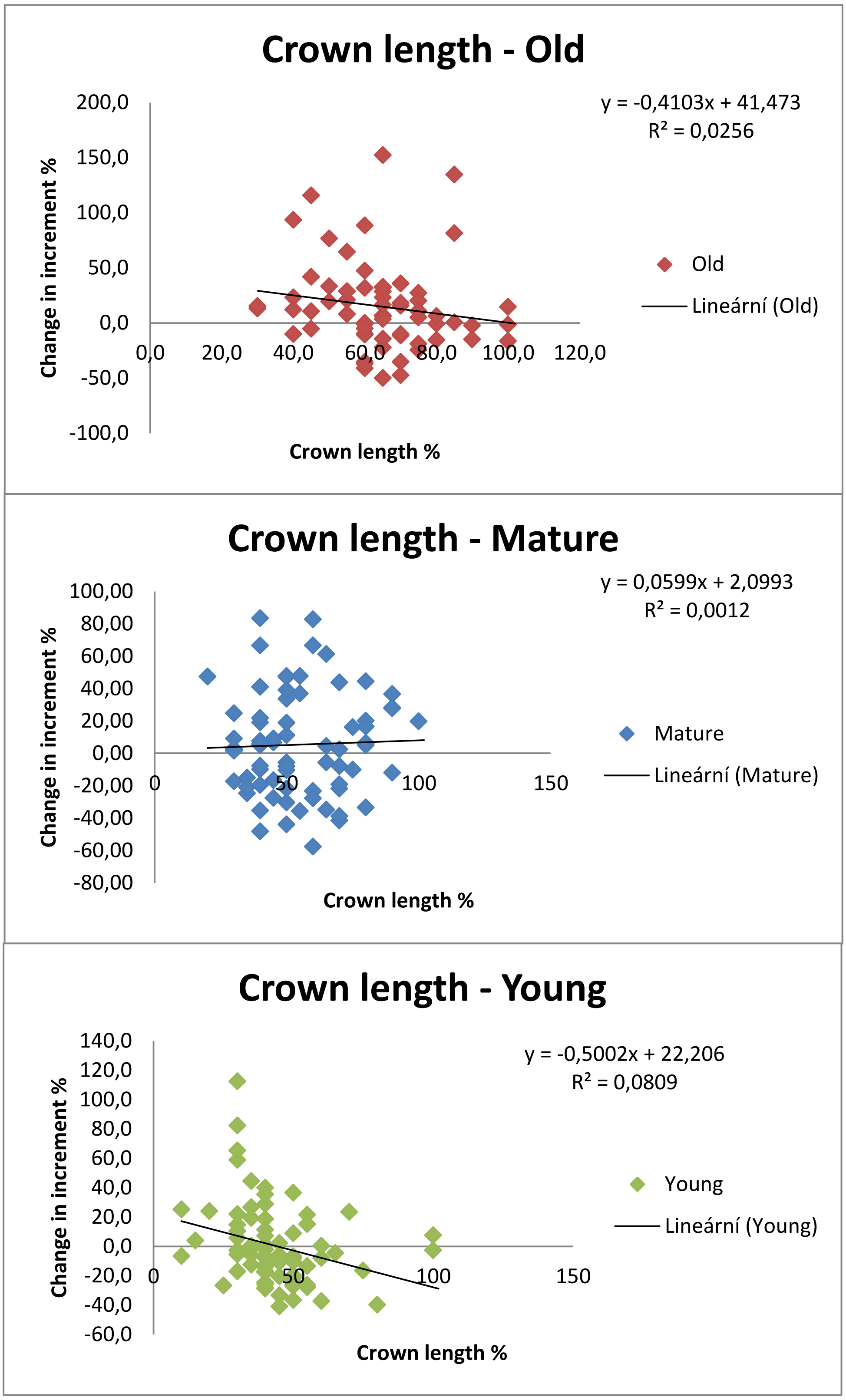

Figure 28: Relation between crown length and change in increment in three different age classes. (N=67, 72, 72)

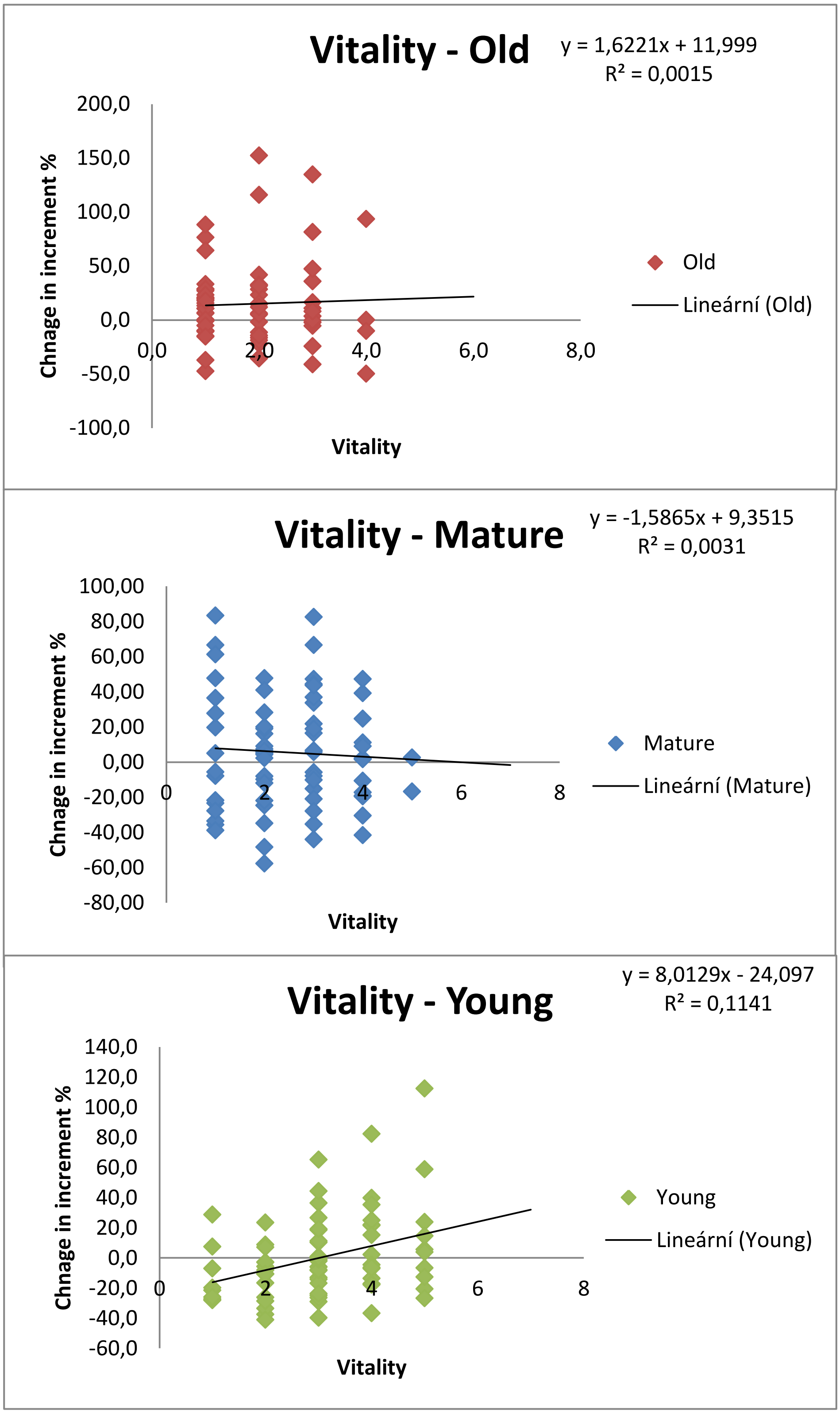

Figure 29: Relation between vitality and change in increment in three different age classes. (N=67, 72, 72)

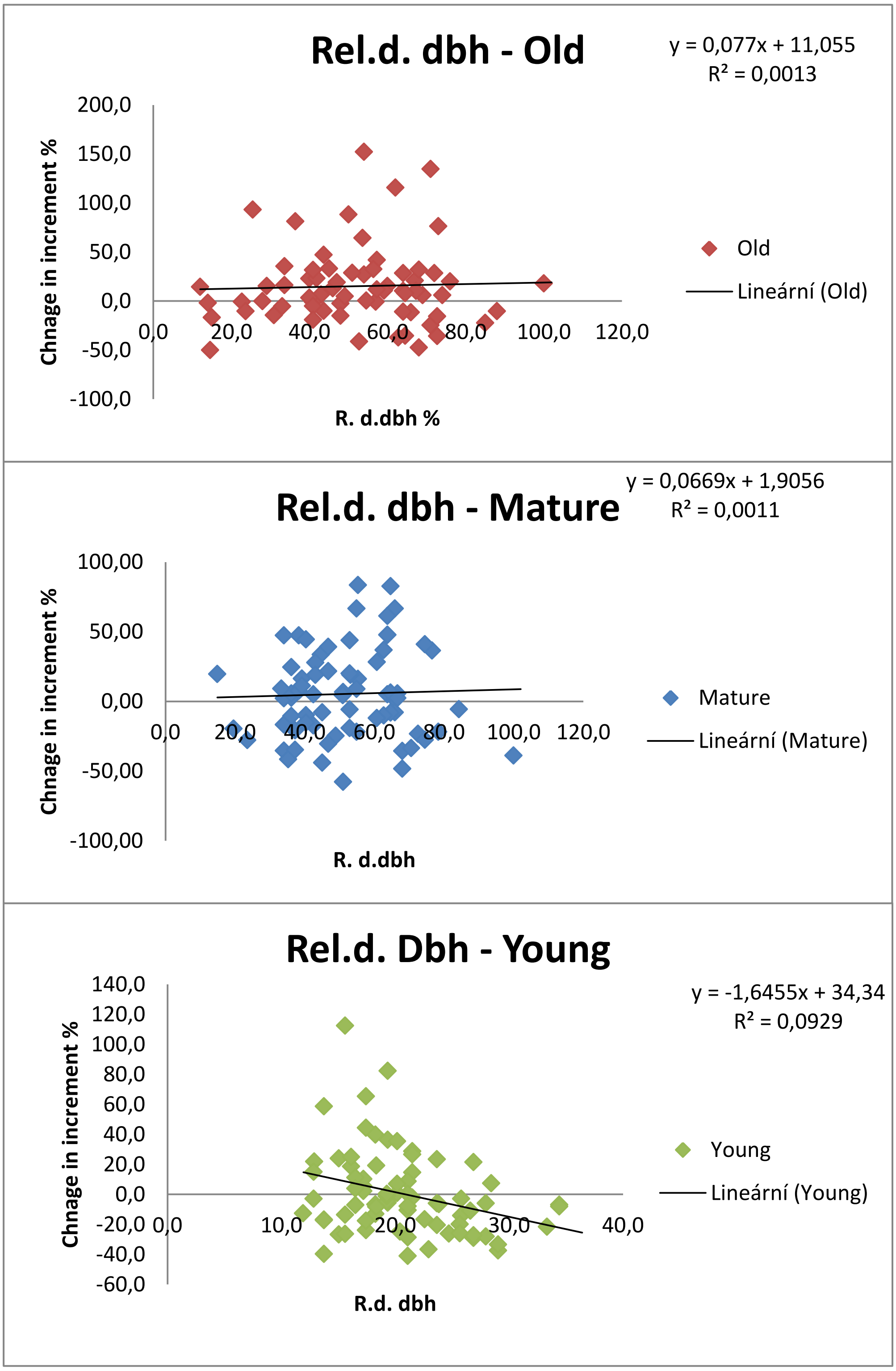

Figure 30: Relation between relative dimension dbh and change in increment in three different age classes. (N=67, 72, 72)

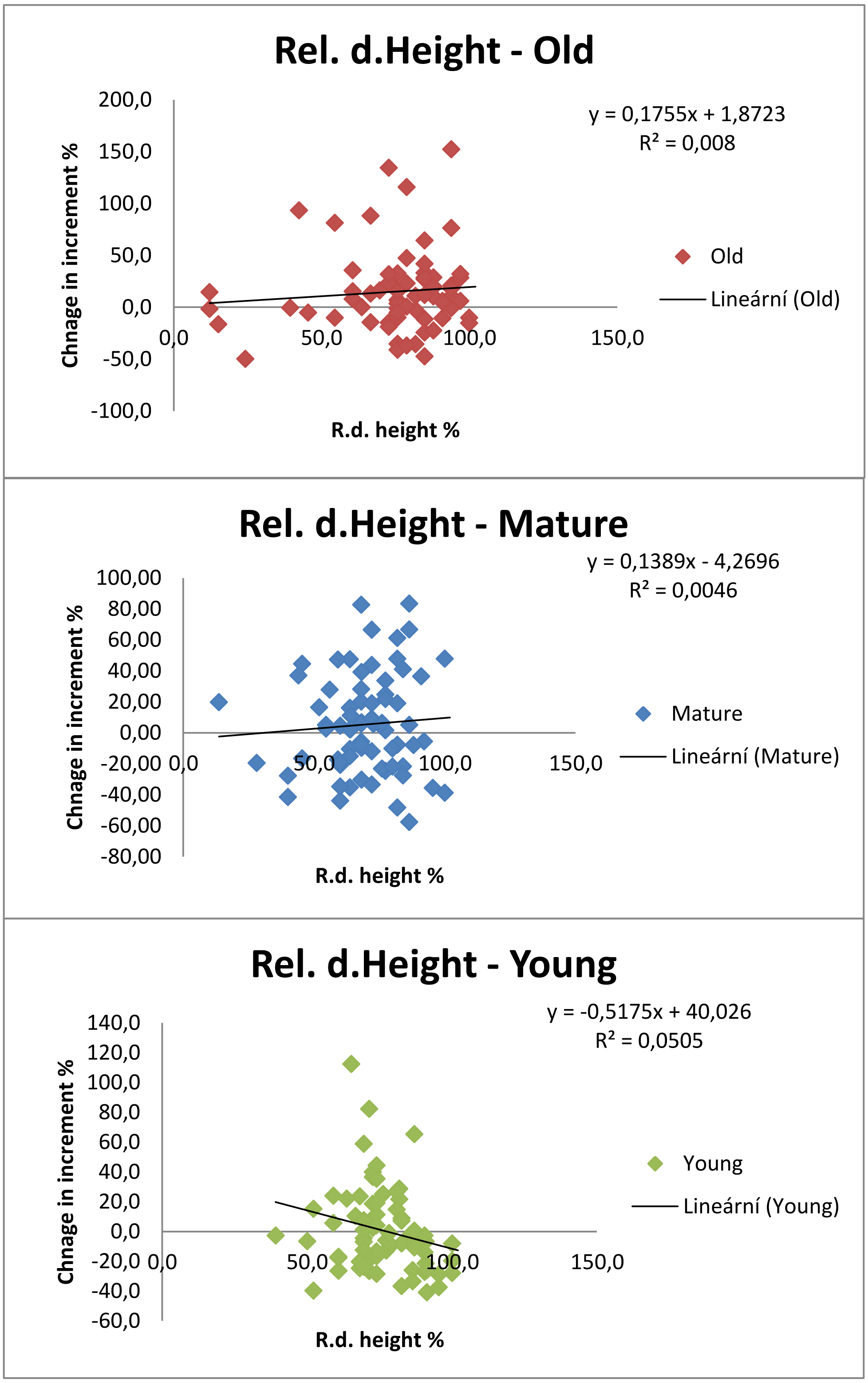

Figure 31: Relation between relative dimension height and change in increment in three different age classes. (N=67, 72, 72)

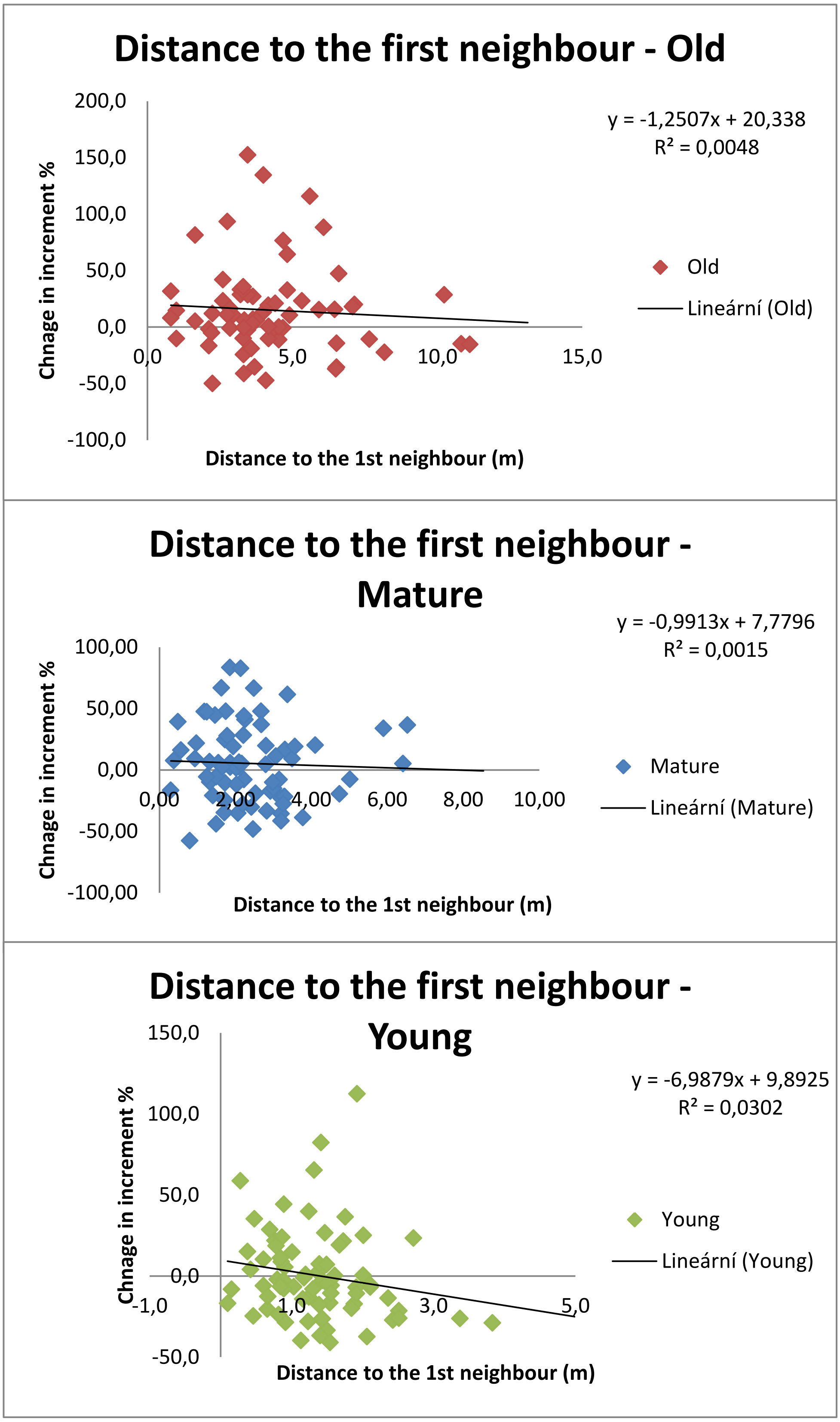

Figure 32: Relation between distance to the first neighbour and change in increment in three different age classes. (N=67, 72, 72)

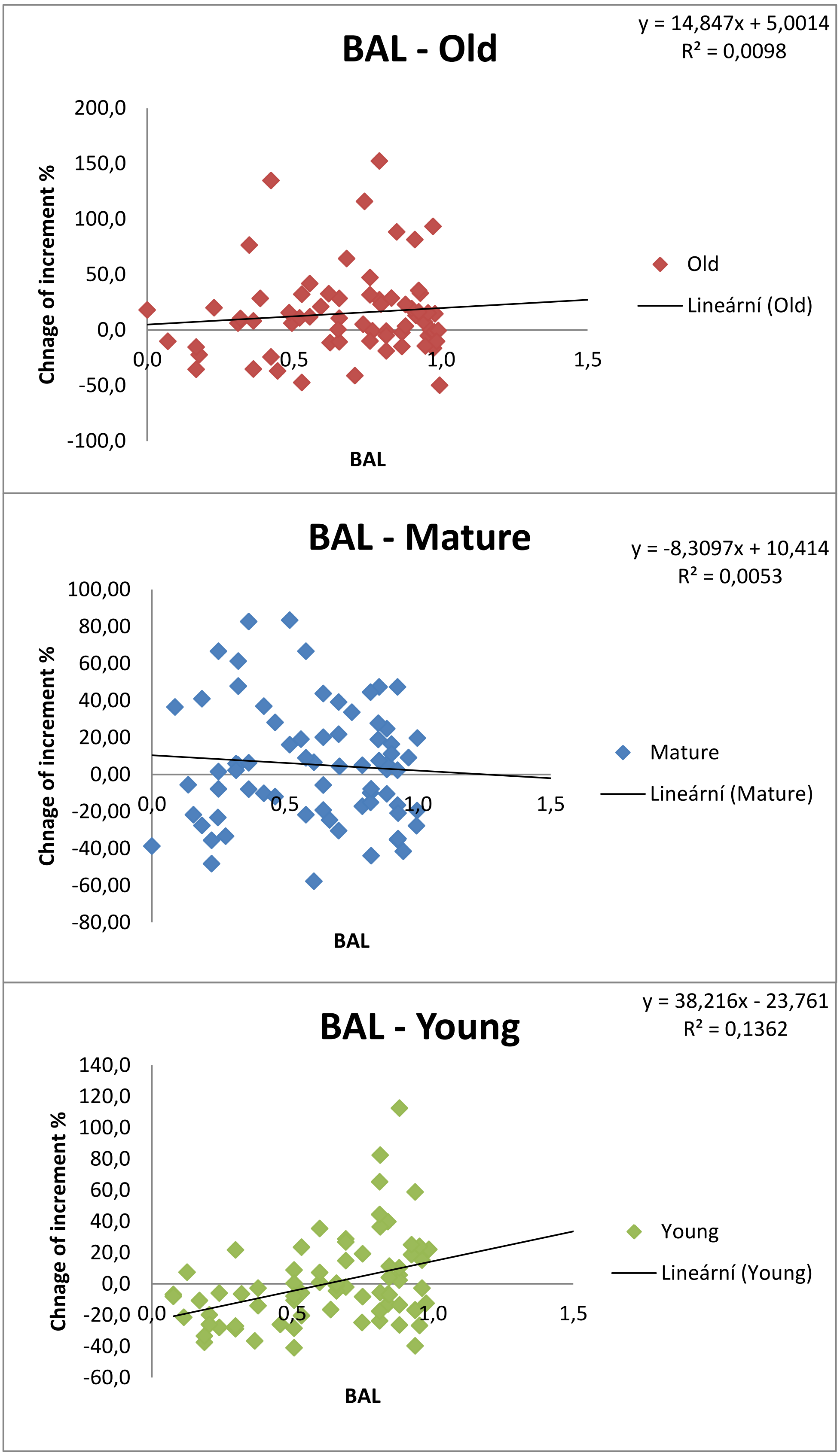

Figure 33: Relation between basal area of larger trees and change in increment in three different age classes. (N=67, 72, 72)

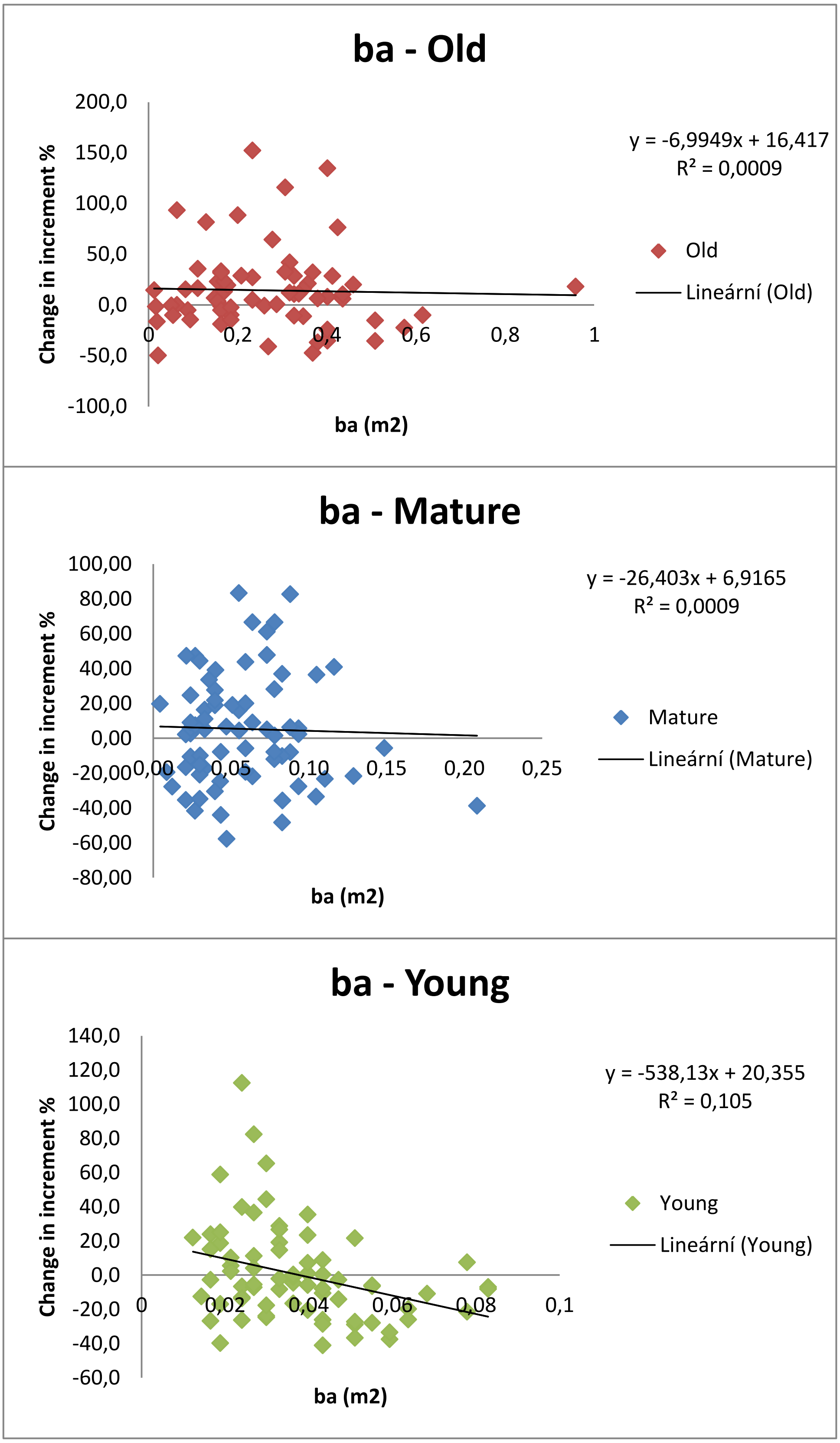

Figure 34: Relation between basal area and change in increment in three different age classes. (N=67, 72, 72)

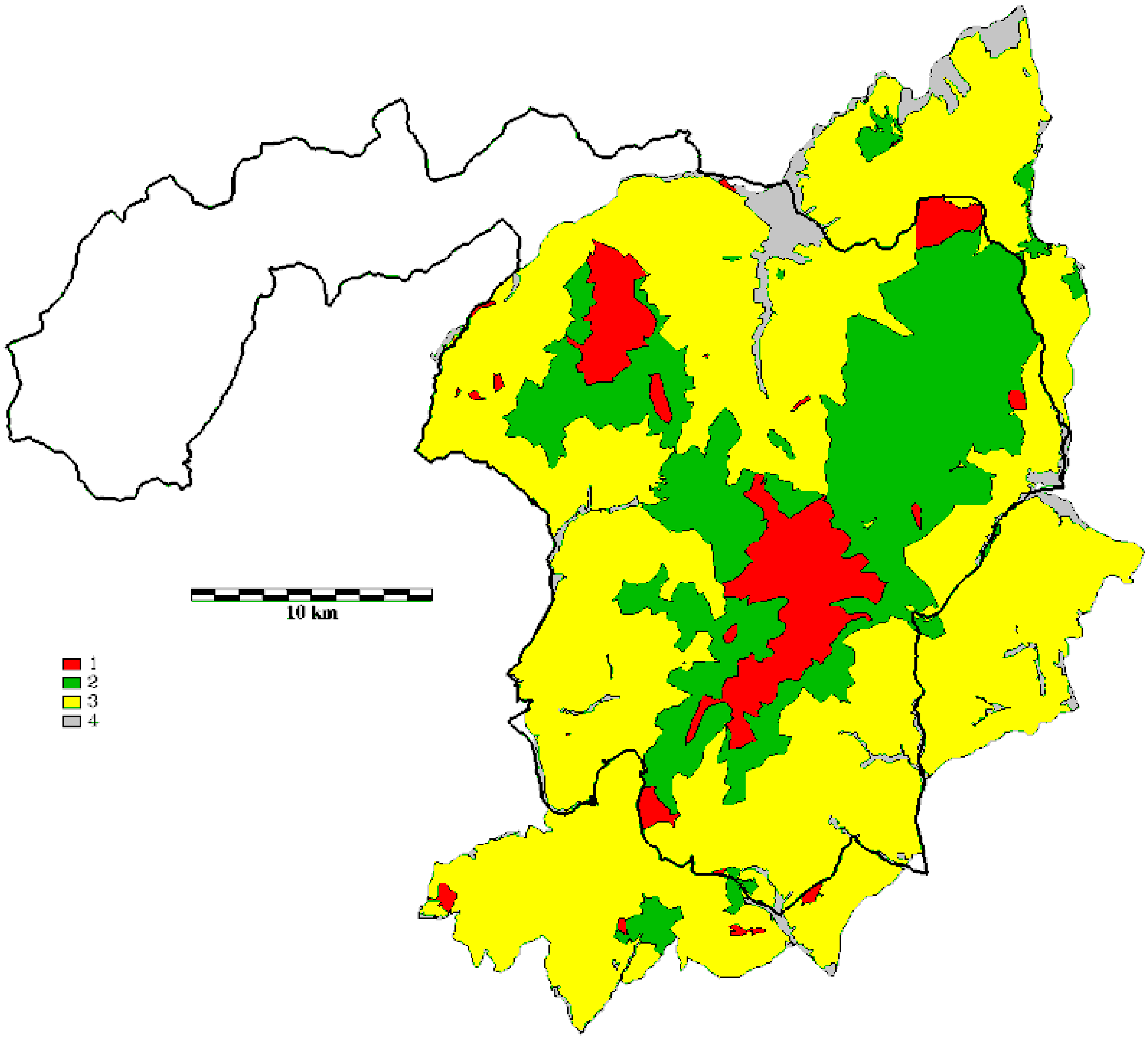

Figure 35: Distribution of four protection zones in the whole region of Protected landscape area - Jeseniky. Number one represents regions with highest level of protection – red labelled,
Source: Adam, J. (2013) Přírodní lesní oblasti České republiky [online]. [cit. 3.4.2015]. Available at WWW: http://www.infodatasys.cz/lesnioblasti/27ZO.gif

Data sampling Form MSc. Thesis - Praděd National Nature Reserve

Location description

GPS coordinates	
Altitude	
Slope	
Exposition	

Transect description

Number	
Direction	
Age class	

Remarks

Tree measurements

Number	Transect Partition	Azimuth	Distance	DBH	Crown length	Stem Damages	Vitality	Height.	Core Num.