Mendel University in Brno

Faculty of Forestry and Wood Technology

Department of Forest Botany, Dendrology and Geobiocoenology

Effect of competition on resprouting and sprout growth of temperate trees

Diploma thesis

Thesis supervisor

Author of thesis

Ing. Radim Matula, Ph.D.

Bc. Lukáš Patra

Declaration

I hereby declare that, this diploma thesis entitled Effect of competition on resprouting

and sprout growth of temperate trees was written and completed by me. I also

declare that all the sources and information used to complete the thesis are included in

the list of references. I agree that the thesis could be made public in accordance with

Article 47b of Act No. 111/1998 Coll., Higher Education Institutions and on

Amendments and Supplements to Some Other Acts (the Higher Education Act), and in

accordance with the current Directive on publishing of the final thesis.

I am aware that my thesis is written in accordance to Act. 121/2000 Coll., on Copyright

and therefore Mendel University in Brno has the right to conclude licence agreements

on the utilization of the thesis as a school work in accordance with Article 60(1) of the

Copyright Act.

In Rrno on:

Before concluding a licence agreement on utilization of the work by another person, I

will request a written statement from the university that the licence agreement is not in

contradiction to legitimate interests of the university, and I will also pay a prospective

fee to cover the cost incurred in creating the work to the full amount of such costs.

m bino on.	

signature

Acknowledgements

First and foremost, my sincere appreciation goes to my supervisor Ing. Radim Matula, Ph.d., for his great insight, tremendous encouragement, high level of support and immense patience. His invaluable knowledge and guidance has been instrumental and very help full. I also thank to Ing. Martin Šrámek, Ph.D., Ing. Martin Svátek, Ph.d., Ing. Jakub Kvasnica and others who helped me with the in field data collection and provided me with their own data from inventories. And of course, magnificent gratitude goes to my family and to all loved ones who helped me and boosted me with their friendship, love and support during the thesis preparation. I am also thankful to the IGA project LDF PSV 2016005 "Woody plants growth and herb vegetation dynamics in coppice in relation to stand structure and soil water regime" for providing financial resources for my fieldwork.

Title: Effect of competition on resprouting and sprout growth of temperate trees

Abstract:

Presented thesis is focused on competition, sprout growth and resprouting ability of

temperate trees. The main aim was to analyse the effect of competition on resprouting

success and sprout growth of selected trees. Calculations are based on sprout size

measurements of selected resprouting trees on pre-existing TARMAG II experimental

plot near Sob šice, the Czech Republic. Appropriate allometric equations were used to

determine biomass of individual trees and pre- and post-harvest competition indices.

Statistical analysis disclosed that pre-harvest and post-harvest competition can

significantly affect sprout growth of temperate trees, but can differ among species and

has variable effect onto the growth. Results also clearly showed that pre-harvest

competition did not affect resprouting ability of Quercu spetraea. The results indicate

that thinning of sprouts in the early stage of coppice development could support sprout

growth and thus biomass production.

Key worlds: Competition, sprout, resprouting, growth, shading, crowding

Název: Efekt kompetice na r st výmladk a výmladnou schopnost strom mírného

pásma

Abstrakt:

P edkládaná diplomová práce je zam ena na kompetici, r st výmladk a výmladnou

schopnost strom mírného pásma. Hlavním cílem bylo analyzovat vliv kompetice na

výmladnou schopnost a r st výmladk . Pomocí, m ení základních charakteristik

výmladk a použitím alometrických rovnic vypo ítat biomasu a p ír st výmladk a také

vypo ítat p ed a po-t žební kompeti ní indexy na již založené výzkumné ploše

TARMAG II nedaleko Sob šic v eské Republice. Analýza odhalila, že p ed-t žební a

po-t žební kompetice m že významn ovlivnit r st výmladk strom mírného pásma,

liší se však mezi jednotlivými druhy d evin a také r zným vlivem na r st výmladk .

Rovn ž se ukázalo, že p ed-t žební kompetice neovliv uje výmladnou schopnost dubu

zimního. Výsledky nazna ují, že probírky v rané fázi vývoje pa ezin by mohly zlepšit

r st výmladk a tak i produkci biomasy.

Klí ová slova: Kompetice, výmladek, r st, výmladná schopnost

TABLE OF CONTENTS

1 INTRODUCTION	1
2 AIMS AND OBJECTIVES	3
3 GENERAL OVERVIEW	4
3.2 Sprouts and sprout growth	4
3.3 Sprouts in forestry	6
3.4 TARMAG II (according to Kadavý et al.)	9
3.4.1 Natural conditions of TARMAG II site	12
3.5 Competition	15
3.6 Field map technology (IFER, Ltd., Jílové u Prahy, Czech Republic)	18
4 MATERIALS AND METHODS	19
4.1 Study area	20
4.2 Data collection	20
4.3 Data analysis	21
5 RESULTS	25
5.1 Effect of competition on biomass production and increment	25
5.1.1 Effect of competition on biomass production	27
5.1.2 Effect of competition on increment	31
5.1.3 Effect of surrounding trees to increment and biomass production	36
5.1.4 Effect of standards to sprout biomass production	38
5.2 Resprouting ability	39
6 DISSCUSION	44
7 SUMMARY	50
8 SHRNUTÍ	51
9 REFERENCES	52
10 LIST OF TABLES AND FIGURES	
10.1 List of tables	
10.2 List of figures	
11 APPENDICES	
11 1 List of appardices	50

1 INTRODUCTION

Temperate forests are dominant ecosystems in areas of mild climate, where the influence of mid geographical latitude is distinctly demonstrated by the summer and winter seasons (Jeník, Pavliš 2011). Trees in such ecosystem can be generally characterized as a plants which, when undisturbed, develop a single, erect woody trunk (Ng 1999, Tredici 2001). However, by anthropogenic disturbances such as logging operations or natural disturbances such as fires, windrows, etc. trees can develop a secondary trunks by the use of natural mechanism of persistence called resprouting (Bond, Midgley 2001). Resprouting or ability of trees to develop sprouts as secondary trunks are in general responses to an injury of primary trunk or root system. They can also be caused by the displacement of primary stem out of the normal vertical orientation or by a dramatic change in surrounding environmental conditions (Helle 1999, Tredici 2001). Therefore, when the aboveground biomass is destroyed or damaged, woody species with the ability to resprout ("resprouters") quickly recover by producing sprouts, whereas species without sprouting ability ("non-sprouters") need to persist in form of seeds or seedlings, or usually die (Bond, Midgley 2001). Sprouts are mostly produced by dormant buds, which are located in the aboveground or belowground organs or rarely by adventitious buds. Adventitious sprouts are usually weak and tend to be short-lived (Johnson et al. 2002). The sprouts ("resprouters") rely on belowground root systems and carbohydrate reserves of parent tree because of missing or damaged aboveground biomass. Resprouters utilize already established and functional root systems and nutrition reserves of undamaged organs of mature tree. Sprouts can, therefore, re-grow more easily and faster and outcompete seedlings (Matula et al. 2012). The occurrence of sprouts after an outbreak or disturbance depends on the sprouting (resprouting) ability of the trees, which differs among and within species (Tredici 2001). The sprouting ability of temperate trees mainly relies on the viability of dormant buds from which new sprouts are produced (Tredici 2001; Johnson 2002) and which decrease with size and age of tree (Matula et al. 2014). According to Kabeya and Sakai (2005) sprouting ability also depends on carbohydrate storage in roots and the remaining aboveground biomass.

Competition as the interaction of two or more organisms or species, which adversely affect each other (Mze 1995), is according to Coats *et al.* (2009) one of the key mechanisms which affect structure and composition of forest and also influences

the tree growth, reproduction and mortality. Aboveground competition (for light) and belowground competition (for nutrients and water) among trees can lead to changes in growth rates and also causes their death (Coats *et al.* 2009). From that it is possible to suggest that competition among trees may affect their sprouts and sprouting ability. To prove this suggestion, pre-harvest and post-harvest data of temperate trees from three inventories (2008, 2012 and 2015), which took a place at TARMAG II experimental plot, were tested.

Firstly, the competition and its possible effect on sprout growth (biomass and increment) of temperate trees were tested. For that purpose three hypothesized effects were assessed: the possible effect of pre-harvest crowding (pre-harvest competition calculated with DBH) on sprout growth, the potential effect of pre-harvest shading (competition calculated with length of live crown) on sprout growth and the effect of post-harvest shading (competition calculated with height of the highest sprout) on sprout growth.

Secondly, the competition was tested for its potential effect on resprouting. According to Kabeya, Sakai (2005) crown competition (shading by its neighbours) decreases the light availability for the tree. On that basis a hypothesis can be assumed that pre-harvest shading (competition calculated with length of live crown) can have an effect on the resprouting ability of trees as well as that an increase in stem competition (crowding) from neighbouring trees can decrease the nutrient availability for the tree (Kabeya, Sakai 2005). On that account, we can assume that increasing pre-harvest crowding (competition calculated with DBH) increases the sprouting ability of temperate trees because of lack of nutrients that can lead to boosting the resprouting ability. Furthermore, dendrometrical characteristics such as diameter at breast height (DBH) and total tree height were used as variables to determine whether they also have an effect on resprouting ability. It is also to be determined whether tree size characteristics or competition have a greater effect on the resprouting ability of temperate trees.

2 AIMS AND OBJECTIVES

The main aim of this diploma thesis was to statistically analyse the effect of competition on resprouting success and sprout growth of selected trees. The goal was also to calculate biomass of individual trees and pre and post-harvest competition indices, using measurements of the sprout size in Sob šice experimental plot (TARMAG II) and appropriate allometric equations.

3 GENERAL OVERVIEW

3.2 Sprouts and sprout growth

Plants reproduce naturally in two different ways (Svoboda 1952): sexually by seeds (generative reproduction) and by parts of plants (vegetative reproduction). Vegetative reproduction (regeneration) covers wide variety of mechanisms that plants have evolved for asexual reproduction (Harper 1977). One of these mechanisms is sprouting. The term sprout or sprouting (Figure 1) describes the process whereby a tree develops secondary replacement trunks (Tredici 2001). In general, a tree can develop secondary trunks (sprouts) in response to injury to its primary trunk or root system (Hallé 1996, Tredici 2001). According to Tredici (2001) all broadleaf trees (angiosperm trees) of temperate zone can crate sprouts, predominantly in initial stage of development (< 15 cm DBH), and many species retain this ability into adulthood (> 15 cm DBH), on the other hand most conifers completely lack this ability. It is only yew (*Taxus bacata*) that naturally creates sprouts in the Czech Republic.

According to Johnson et al. (2002) we can distinguish sprouts, which originate from dormant buds or adventitious buds. Sprouts that originate from dormant buds are connected to the pith of the tree by elements called bud traces (Liming 1942). They usually remain neglect in dormant state unless their vascular connections are severed by cutting or otherwise interrupted (Vogt, Cox 1970). There are several forms of sprouts originating from dormant buds such as stump sprout, seedling sprouts and grubs (Johnson et al. 2002). Stump sprouts grow from dormant buds at or near the base of the stump of a cut tree. Seedling sprouts can grow from dormant buds located anywhere along the stem between the root collar and the terminal bud cluster. Grubs are sprouts, which grow from dormant buds on the large, mature root systems and usually do not have any aboveground stumps. Sprouts that originate from adventitious buds are formed from callous tissue around wounds or other tissues and unlike dormant buds do not have bud traces extending to the pith of the tree (Johnson et al. 2002). Stool sprouts and root sprouts, these are two main sprout forms, which originate from adventitious buds. Stool sprouts develop adventitiously and directly from the cut or wounded surfaces of stumps. Root sprouts develop similarly from adventitious buds on roots. Adventitious buds are usually weakly attached to the stump and also tend to be either short-lived or rarely occur at all (Johnson et al. 2002).

According to Tredici (2001) it is more significant when and in which part of the tree life cycles sprouting occurs (ecological perspective) than is the origin of the sprout (morphological perspective). From this ecological point of view it is possible to distinguish juvenile seedling and saplings sprouts, sprouts of mature trees that originated as a response to logging operations and sprouts of mature trees originated as a response to non-logging disturbances. The most important sprouts of mature trees from forestry and forestry operations point of view are the ones that originated as a response to logging operations. When trees are felled and there is still a sufficient content of storage compounds in the root system, the tree sap is then forced upwards, but cannot penetrate dead tissues and so remains in the basal part of the stem and induces the formation of sprouts (Mad ra, Martínková 2009). Newly growing sprouts can uptake large amounts of nutrients from stumps and so grow faster at initial stages of growth - much faster than seedlings. Therefore culmination of height increment comes much earlier than in plants that originated from seed (Svoboda 1952). The rate of bud branching and bud mortality changes with the age, size of the tree and geographical conditions. The balance of these variables can be partially determined by their spatial distribution and the total number of sprouts. Some buds fail to produce sprouts simply because of the physical resistance of the bark (Johnson et al. 2002). Sprouting is common and important for traditional coppice management of woodlands in both temperate and tropical forests (Bond 2001).

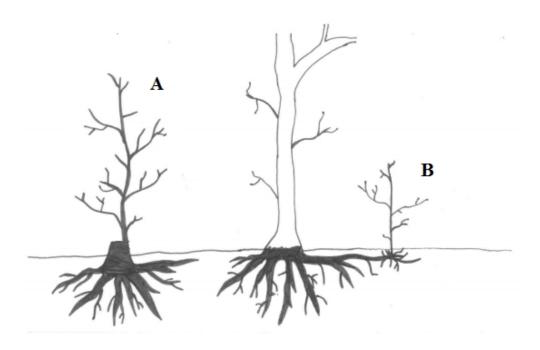


Figure 1 Drawing by Lukáš Patra depicting sprout originate from: A stump, B root

3.3 Sprouts in forestry

According to Ministry of Agriculture Decree no. 83/1996 Coll., of forest Act no. 289/1995 Coll., forests in the Czech Republic can be divided by their form or shape of into three types as follows: high forest, coppice forests, coppice with standards.

1. High forests

High forest (seed forest, high stem forest) is form of forest, which originated by natural regeneration (by seeds) or artificially by human intervention (by seeding, seedlings or planting) (Kadavý *et al.* 2011). High forest is the predominant and the most widely implemented form of forest management in the Czech Republic. Generative renewed stands grow slower than the sprouts in their initial phases, but they have a better quality (straighter) and stronger wood in stems. High forests are generally characterized by a long rotation period (at least 90 to 100 years) and large, tall mature trees with a closed canopy (Kadavý *et al.* 2011). The average rotation period of high forest in the Czech republic is 114,8 years. In term of wood production high forests are characterized by high percentage of logwood (Kadavý *et al.* 2011).

2. Coppice forests

Coppice forest is form of forest, which is systematically restored by vegetative reproduction of sprouts. These usually come from dormant buds on roots and tree stumps. Coppice forests are single storey forests (Polanský 1956). Sprouts are highly accretive due to already developed root systems of stumps. Forests that originate from sprouts are characterized by growing in bunch or clusters and also by "sickle" shape stems near to its bottom. Due to its development this bunch or cluster growth character is lost (Kadavý et al. 2011). Rotation of the coppice forests ranges from 5 years (willow osier plantations), up to 40 years for oak (*Quercus* sp.), beech (*Fagus* sp.) or hornbeam (*Carpinus* sp.) stands and even up to 60 years in case of alders (*Alnus* sp.). The rotation period is determined by the sprouts, tree species, the amount of expected production and also by natural conditions of the area (fertility) (Poleno 1994). Wood that is harvested from a coppice forests is of significantly lower quality, usually is with knots and have worse technical characteristics than high forest wood. Total production of vital, well-developed coppice forest corresponds to high forest production, but economic value of wood is significantly lower (Polanský 1956). According to Kadavý et al. (2011) coppice

forest forms are distant to naturally developed forest ecosystems. Often repeated and almost complete removal of biomass deeply extends into the material cycle while short rotation periods maintain coppice forests in phase of re-growth or recruitment. Coppice forests, from the historical perspective, are known to people since the beginning of woodworking and first forest activities in Neolithic age (Bu ek 2010). People used the ability of trees to create sprouts for as far as can be documented, mainly for the purposes of easily accessible firewood, for building purposes, charcoal manufacturing etc. The major purpose of coppice forests stems mainly from reason that people could easily carry small stems and twigs back to their homes without necessities of using machines or animals. Coppice forests were probably preserved in some places due to this accessibility (Bu ek 2010). The oldest historical evidence of coppice forests in the Czech Republic is from Mikulov and Lednice forests inventory lists dated to 1384 (Noti ka 1956 in Bu ek 2010). These lists contain data such as the names of the forests, their age and also rotation periods, which were, for example, in Liechtenstein coppice forests 7-years. The very short rotation periods were probably driven by the needs for firewood (Bu ek 2010). The lack of wood of bigger dimensions led to the replacement coppiced forests by high forests over time. From the point of view of recent history the area of coppice forests in the Czech Republic constantly declines. In the beginning of twentieth century coppied forest covered more than 4% of the forest lands. Today, however, the area of coppice forests cover less than 1% of forests lands (Kadavý et al. 2011).

3. Coppice with standards (C-W-S)

According to Kadavý *et al.* (2011) coppice with standards are multi-storey forests, where the lower storey is composed of coppices stands (vegetative origin) and the higher storey is composed of standards (seed trees) of either generative or vegetative origin. Lower storey of coppice with standards forest is usually composed of broadleaf, shade tolerant species with good sprouting potential such as lime (*Tilia* sp.), maple (*Acer* sp.), elm (*Ulmus* sp.), hornbeam (*Carpinus* sp.), but also of few light demanding species such as oaks (*Quercus* sp.), chestnuts (*Castanea* sp.), alders (*Alnus* sp.), and ashes (*Fraxinus* sp.). Upper storey is usually formed by economically valuable species; for instance oaks, maples, elms, larches (*Larix* sp.), poplars (*Populus* sp.) or birches (*Betula* sp.). At the time of lower storey harvest (usually each 30 - 50years), few best sprouts or trees originating from seed are left uncut (or planted), to form a future upper

storey. This process leads to creating 3 or 4 successive generations of standards. So called "false" coppice can also be distinguished. Standards of such forest stands originated from the best sprouts and form an even aged upper storey, thus false stem wood is crated. Nowadays, the standards (seed trees) are selected exclusively from seed originated individuals, due to better quality and better growth characteristics. A standard (seed tree) should be a subject to general qualitative requirements such as perfect health condition, straight trunk of at least 6 m in length and long dense and healthy crown. Several types of coppice with standards forests (c-w-s) can be distinguished according to the numbers of standards per area - standing volume (Polanský *et al.* 1956; Kadavý *et al.* 2011):

- i. low standing volume ($< 100 \text{ m}^3\text{ha}^{-1}$) with number of standards ($50 100 \text{ trees} \cdot \text{ha}^{-1}$)
- ii. medium standing volume $(100 200 \text{ m}^3\text{ha}^{-1})$ with number of standards $(100 160 \text{ trees} \cdot \text{ha}^{-1})$,
- iii. high standing volume $(200 400 \text{ m}^3\text{ha}^{-1})$ with number of standards $(160 200 \text{ trees} \cdot \text{ha}^{-1})$

The coppice with standards forest are difficult to manage due to technical silvicultural practices as controlling the species composition, standard standing volume, etc. These practices should maintain an optimal relationship between the upper storey and the lower storey of forest (Kadavý *et al.* 2011).

3.4 TARMAG II (according to Kadavý et al.)

TARMAG II experimental site is situated in the Czech Republic (GPS coordinates: 49°14'43"N, 16°35'59"E) approximately 2 kilometres southwest from the village of Sob šice, in the southern Moravian region near city of Brno. Site was established at the turnover of 2008 and 2009 as the second of its kind. Its main purpose is to simulate the influence of coppice and coppice with standards stands on biodiversity. It was created as part of the Ministry of the Environment of the Czech Republic (MoE CZ) project called Biodiversity and Target Management of Endangered and Protected Species in Coppices and Coppices-with-Standards included in the System of NATURA 2000 (Kadavý et al. 2011). TARMAG II experimental plot belongs to The Training Forest Enterprise K tiny of Mendel University in Brno (TFE) and is situated in Vranov forest district. It is not the only kind of such experimental site under the Training Forest Enterprise K tiny. TARMAG (Hády) experimental research plot of the same purpose was established earlier in 2008 at the K tiny Training Forest Enterprise Bílovice Forest District (GPS coordinates: 49°13′29.87″N, Masaryk v les, 16°40'55.391"E).

TARMAG II experimental site belonged to the forest stand type 80C7 before conversion, which was included in management set of stand No. 205 (exposed oak habitat with special purpose of lower altitudes), with a rotation period of 130 years and a regeneration period of 30 years. The forest stand before logging interventions had a character of upcoming false stem woodland and was described according to current forest management plan (2003 - 2012) as fully stocked single storey high forest, with closed canopy. Predominant forest type on the experimental site was 1B1 which can be described according to Czech forest typology as rich hornbeam-oak steppe on plateaus and rounded ridges with *Carex montana* with prevailing typical mesotrophic cambisols (KMm^b) with sandy-clay and gravel soil type and granodiorite substrate. In lesser extend was also 1C2 (dry oak-hornbeam forest on the slopes with *Carex* sp.) forest type represented on site. The forest stand was about 72 years old just before the logging operations took place in 2009.

Table 1 Trees species composition on TARMAG II experimental site before conversion, according to Kadavý *et al.* (2001). Adjusted by Lukáš Patra

G	Quantity	Volume
Species	(no. of trees)	(m ³ over the bark)
Quercus petraea	2707.000	889.820
Pinus sylvestris	44.000	22.480
Carpinus betulus	43.000	2.380
Pinus nigra	13.000	5.040
Tilia cordata	13.000	2.300
Larix decidua	13.000	3.620
Quercus robur	9.000	1.930
Acer campestre	7.000	0.100
Prunus avium	4.000	0.270
Sorbus torminalis	3.000	0.170
Acer platanoides	2.000	0.070
Tilia platyphylos	2.000	0.020
Pyrus communis	1.000	0.020
Picea excelsa	1.000	0.020
Pinus strobus	1.000	0.010
Total	2863.000	928.230
Average/ha	716.000	232.060

Fifteen different types of woody species were measured on TARMAG II experimental site before logging operations and its conversion. It can be noted in Table 1 that total number of trees was 2883, which had a total volume of 928.23 m³ (measured over the bark). The most dominant specie was sessile oak (*Quercus petrea*) whose representation on site reached 96% of the total number of trees. The second most frequently occurring tree species was Scotch pine (*Pinus silvestris*) with 44 trees followed by hornbeam (*Carpinus betulus*) with 43 trees. Black pine (*Pinus nigra*), larch (*Larix decidua*) and small leaved - lime (*Tilia cordata*) occurred in numbers of 13 trees each. Maple (*Acer campestre*), spruce (*Picea abies*), mountain-ash (*Sorbus torminalis*) and etc. occurred on site only in small numbers (< 10).

The design and the establishment of TARMAG II experimental site followed a similar design pattern formerly used in TARMAG (Hády). The whole site covers an area of 4 hectares (200 × 200 m). This area was divided into 16 cells. Each of them is the size of 50 m by 50 m. In addition, a control area was created in a protection zone of TARMAG II. This control area does not have precisely defined geometric shape, but measuring 79 trees of various storeys selected it. Four different types of felling intensities were used as seen in Figure 2: clear cut (cells No. 1, 3, 9 11), very high

intensity felling (cells No. 6, 8, 14, 16), high intensity (cells No. 5, 7, 13, 15) and medium intensity (cells No. 2, 4, 10 and 12). Each four neighbouring cells (in total 100 x 100 m) represented these four felling intensities and therefore various numbers of standards.

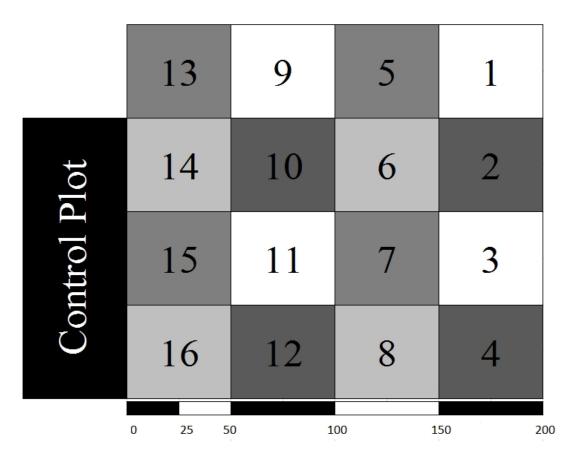


Figure 2 TARMAG II felling intensities according to Kadavý *et al.* (2009). Where white represents the clear cut (perspective: coppice), light grey represents very high felling intensity (perspective: coppice with standard with low standing volume and a small number of standards), grey represents high felling intensity (perspective: coppice with standard with standard standing volume and an average number of standards) and dark grey represents medium felling intensity (perspective: coppice with standard with standard standing volume and a high number of standards). Adjusted by Lukáš Patra

According to Kadavý *et al.* (2009) all trees with DBH of at least five centimetres (> 5 cm) were measured in TARMAG II experimental site, similarly to the TARMAG (Hády) site, and recorded into database. The measured variables were as follows: DBH, total tree height, and living crown bottom. Specific species code was given to every

measured tree. According to the cell plot design, on average 24 standards were marked in cells with very high felling intensity, 35 standards were marked in cells with high felling intensity and 46 standards were marked in cells with medium high felling intensity. The purpose was to achieve a 1:3 ratio between the number of standards in the older and the younger storey. The trees with DBH over the 50 cm (> 50 cm) were not consider to be a good standards due to advanced age. (Kadavý *et al.* 2010). Sessile oak (*Quercus petraea*) as the predominant specie at experimental plot was used as main standards tree. The logging operations took place at the turn of 2008 and 2009 and were performed as whole tree harvest. Undesirable trees were cut down, also all woody vegetation even of shrubby character was removed from the plot and whole trees were transported out of the plot. Logging residues were minimal (Kadavý *et al.* 2010).

3.4.1 Natural conditions of TARMAG II site

1. Geological, geomorphologic and soil conditions

From geomorphologic point of view TARMAG II experimental site belongs into

Precinct: Sob šice uplands (Table 2), which is characterised by rugged relief with deep valleys of the river Svitava. According to Truhlá (1996) an impact of several geomorphologic formations can be distinguished on experimental site. The major influence is represented by Adamov upland formation, which is composed mainly by amphibolic granodiorite and less biotic-

Table 2 TARMAG II experimental site characterization according to geomorphologic division of Czech Republic (Culek *et al.* 2005)

System	Hercynian
Province	Bohemian Massif
Subprovince	Czech-Moravian System
Region	Brno uplands
Unit	Drahanská uplands
Subunit	Adamov uplands
Precinct	Soběšice uplands

acidic granodiorite and diorites. The site is also influenced by Moravian Karst with Devonian and Jurassic limestone covers and with chertic and flint coverings. Pleistocene and loess clays, eluvial and deluvial deposits can be identified as main covering formations on site (Truhlá 1996). Typical mezotrophic cambisols, albeluvisols, rendzic leptosols crossing over to cambisols (in areas with limestone) and haplic luvisols typically on loess clays can be found on TARMAG II experimental site (Culek *et al.* 2005).

2. Climatic conditions

According to Quitt (1971) TARMAG II experimental site belongs into MT11 climatic region, which can be characterised as moderately warm with dry summers, moderately warm springs and autumns and with moderately cold winters. An average annual rainfall is about 520 mm, and the average annual air temperature is about 8,5°C. Average annual number of snow days is 50 - 60 and average number of days with snow cover is also 50 - 60. Average seasonal maximum snow depth ranges from 20 to 30 centimetres. Average annual total global radiation is about 3900 - 4000 MJ/m². The average annual sum of cloud days represented by 60 - 65%. Average annual duration of sunshine is 1600 - 1700 hours and average annual wind speed is 3 - 4 m/s (Tolasz *et al.* 2007).

3. Biogeographical conditions

Experimental site is located in Brno bioregion no. 1.24. on the eastern edge of the Hercynian subprovince, which belongs into Central European Broadleaf Forests province. Thanks to its location the Brno bioregion is also influenced by Pannonian and Carpathian subprovince. In terms of geobiocenology and altitudinal zonation the main vegetational tier of Brno bioregion is the oak-beech vegetation tier followed by significant proportion of beech-oak vegetation also with enclosed occurrence of beech vegetation. Natural forests were largely replaced by spruce monocultures, but at the same time larger complexes of natural hornbeam and beech forests (Svitavy valley) are still locally preserved (Culek *et al.* 2005). The bioregion lies on the boundary of termophyticum and mesophyticum phytogeographical regions whereas two districts can be found as follows Znojmo-Brno Upland, which lies in termophyticum and the Moravian foothills of the Vyso ina at mesophyticum (Culek *et al.* 2005).

4. Flora and founa

The flora within the described area consist mainly in sessile oak (*Quercus petraea*) and hornbeam (*Carpinus betulus*) with frequent additions of beech (*Fagus silvatica*) and also fir (*Abies alba*), sometimes lime (*Tilia cordata*), rowan (*Sorbus sp.*) or maple (*Acer sp.*) etc. Shrubs are frequently represented by hazel (*Corylus avellana*), dogwood (*Cornus sp.*), hawthorn (*Crataegus sp.*) or *Ligustrum vulgare*. Undergrowth synusia is typically demonstrated by wild ginger (*Asarum europaeum*), stilchwort

(Stellaria holostea), sweet woodruff (Galium odoratum), bulbiferous coralwort (Dentaria bulbifera), wood melick (Melica uniflora) and hepatica (Hepatica nobilis) (Culek et al. 2005).

5. Fauna

Fauna of the region is strongly influenced by agglomeration of the Brno city and for that reason an increased occurrence of different synantropic species such as martens (Martes foina) and common kestrel (Falco tinnunculus) can be found. Among the most important species belonging to the region are (Culek et al. 2005): mammals such as european hedgehog (Erinaceus europaeus), marten rock (Martes foina), horseshoe bat (Rhinolophus hipposideros), birds such as sand martin (Riparia riparia), savi's warbler (Locustella luscinioides), penduline tit (Remiz pendulinus), reptiles such as green lizard (Lacerta viridis), smooth snake (Coronella austriaca), amphibians such as salamander (Salamandra salamandra), mollusks such as Cepaea vindobonensis and insects of the like of grasshopper vine (Ephippiger ephippiger), hungarian ground beetle (Carabus hungaricus), Lucanus cervus, magnificent flower beetle (Protaetia speciosissima), etc.

3.5 Competition

Within every biotope, each species uses given conditions of their environment, abiotic factors as well as biotic factors and their characteristics. However, since these environmental factors (water, nutrients) are not unlimited, competitive interactions for natural resources occur (Slavíková 1986). The competition of two or more organisms or species is based on the interaction, which adversely affects each other (same demands for food or nutrients, etc.) (Mze 1995). According to Poleno *et al.* (2011), it is possible to distinguish competition between individuals as follows:

- i. **The intraspecific competition-** contacts, interaction and links between individuals of one species.
- ii. **The interspecific competition** the interaction of two or more species or populations.

It is theoretically possible to assume according to Lašt vka (1986) that competition arises when continuous inflow of energy and substances from environment is somehow interrupted for one or both competitors. Therefore, competitive relations are significantly manifested in the period of needs (emergency). On the contrary when there is a sufficient supply of resources competitive relationships are less significant (Poleno et al. 2011). The major competition factors in natural communities are considered to be water, light and nutrients (Clements, Shelford 1939). However, their significance differs. For example, competition for nutrients is generally more important at an early stage of development of plants. Competition for light is significant in later phases of development (Wilson 1988). Effects of competition can be observed especially as differences in vegetative growth, seed production and mortality (Grimm 2001). When competition occurs it does not result in immediate elimination or death of plant but demonstrates itself in a decrease of metabolism intensity and growth. Plants, unless able to adapt, are though eventually eliminated since competing for one factor sequentially establishes an entire complex of negative effects. Competition is more intensive, where limited energy and metabolic factors are more important to metabolism (Lašt vka, 1986).

Competition indices are used for an evaluation of competition. These indices allow for the assessment of how much is the growth of individual trees in the stand affected by the presence and characteristics of neighbouring individuals. Competition can be expressed as a summary of characteristics of individual tree, or may describe conditions of the environment in the immediate vicinity of individual trees (Morav ík 1993).

According to Munro (1974) we can generally divide competition indices into two main groups according to whether the spatial distribution of individual trees is used or not.

- i. Distant independent competition indices: are based on the characteristics common for the whole stand and use functions of stand-level variables and initial dimensions of the subject tree as stand density measures, total basal area, ratios of a tree dimensions compared to the average dimension in the stand, ratios of a tree dimensions to the average dimensions of the dominant trees, crown ratios and other characteristics. These indices are usually easy to calculate.
- ii. **Distant dependent competition indices**: use the distance and spatial distribution of trees in the stand, which allows expressing the competition in the closest neighbourhood of individual trees in the forest. The amount of influence is then evaluated by the numbers, sizes and distances of adjacent trees. Distant dependent models require tree coordinate location for computations and are used to measure the influence of local neighbours.

Competition of distant dependent models is most commonly based of several principles as explained by Morav ík (1993):

- i. **Zone of influence**: This zone is defined around each tree in the stand. This zone is generally a function of the tree size. Competition, in this case, is assessed according to the size of the area, which overlaps zones of influence of individual trees.
- ii. The size and dimension of neighbouring trees: The competition is calculated from the size (DBH, height) of individual trees or as a function of size and distance.

iii. **Potentially available area**: The area of stand is divided into small segments, which are assigned to individual trees. Potentially available area can have the shape of polygonal or circular sectors or determined otherwise.

There are several types of distant dependent and distant independent competition indices according to Burkhard and Tomé (2012). The most famous and mostly used are as follows:

i. **Distant independent indices**

Relative dimensions: are indices using mathematical formulations, which measure the hierarchical position of subjected tree within the stand.

Proportional to relative tree basal area: are indices, which divide forest stand between the individual trees according to their dimension in relation to the dimension of the average tree.

Crown ratio: is simply crown length divided by total tree height. It is also being used to express the past competition undergone by each tree.

ii. Distant dependent indices

Area overlap indices (**AO**): are the first developed distance-dependent indices and they are based on the sharing of the areas of influence of the subject tree and its competitors. One of the AO indices is Arney's index.

Point density measures (PD): the number of competitors dependent on the basal area and on used factors. One of the PD measures is Spurr's point density.

Distance-weighted size ratio (**DR**): can be defined as the sum of the ratios between the dimensions of each competitor to the subject tree. It is weighted by a function of the inter tree distance. DR types of indices have the advantage of easy calculation, while explaining variation in growth with precision similar to other indices. One of the famous DR index is Hegyi competition index.

Area potentially available index (APA): can be described as the area of the smallest polygon defined by the bisectors to the subject tree and competitor sizes (inter tree lines). The most known APA index is Brown's index.

3.6 Field map technology (IFER, Ltd., Jílové u Prahy, Czech Republic)

Field-Map is a hardware-software technology, which enables fast and efficient data collection in the field and their subsequent office processing and evaluation. Field-Map combines real-time GIS software with electronic device used for mapping and dendrometric measurements. This technology originated in the Czech Republic and is primarily used for forest and vegetation inventories. However, its applications are diverse: from mapping of the landscape to precise surveying of archaeological excavations. Field-map technology is currently used for projects in 28 different countries. As mentioned, it is composed from two parts:

1. Software

The software is the major and most essential part of Field-map technology and it is consist of several modules:

- FM Project Manager is the basic module used in the process of project preparation. It also allows database creation and design based on its own methodology.
- FM Data Collector is used in field computers and tablets. It is an application that directly supports electronic measuring devices and gives users the option of mapping and field measurements. The basic principle is simple. Users record the location and dimensions of trees directly into the computer by using in build GPS to localize initial point in field and with the help of measuring instruments.
- **FM Inventory Analyst** is a module that allows the user to statistically evaluate the measured data, and export the results in the form of graphs and tables.

2. Hardware

The major part of the hardware system is a field tablet or computer on which Field-map software is installed. To this computer are then connected the other electronic measurement devices such as GPS, electronic compass, inclinometer, distance meter etc. The measurements are transmitted online into the computer where the data are automatically processed and visualized in form of digital map. There are many different possible combinations solely depends on the type and needs of a particular project.

4 MATERIALS AND METHODS

Data collection for this diploma thesis took place at TARMAG II experimental site near Sob šice (Figure 3), in Moravian region near Brno in the south eastern part of the Czech Republic (49°14'43"N, 16°35'59"E). This study plot belongs to The Training Forest Enterprise K tiny of Mendel University in Brno (TFE) and is situated in Vranov forest district. Since its establishment it served as a foundation for a project, by the Ministry of the Environment of the Czech Republic (MoE CZ), called 'Biodiversity and Target Management of Endangered and Protected Species in Coppices and Coppiceswith-Standards included in the System of NATURA 2000 (Kadavý *et al.* 2011). The author of this thesis, therefore, practically follows upon and continues with previously established measurement methods carried out since the establishments of this study plot. The author participated in two inventories that took place in 2013 and 2015.



Figure 3 TARMAG II research plot. Data taken from Google maps 2016, adjusted by Lukáš Patra

4.1 Study area

The total area of TARMAG II plot is 4 hectares and its average elevation is about 355 meters above sea level. The geological conditions of the site feature granodiorite bedrock and Cambisol soils (Culek et al. 2005). According to (Quitt 1971) the study site belong into MT11 climatic region which can be characterised as moderately warm with an average annual rainfall of about 520 mm, and the average annual air temperature of about 8,5°C. The most dominant species occurring on plot prior to and post conversion is *Quercus petrea* (hereinafter referred to as the *Quercus*) followed by scots pine (*Pinus silvestris*), *Carpinus betulus* (hereinafter referred to as the Carpinus) and Tilia cordata (hereinafter referred to as the Tilia). TARMAG II site was measured in 2008 where large pre-harvest inventory was created by using Field-map technology (IFER, Ltd., Jílové u Prahy, Czech Republic). Exact positions (X,Y,Z coordinates) were measured for each individual tree with DBH > 5 cm and main dendrometric data such as diameter at breast height (DBH), height, height of the base of live crown were taken. The high forest was harvested at the turn of the year 2008 and 2009. Logging operations were performed as whole tree harvest (Kadavý et al. 2010). The study area was fenced to prevent game damage. Four years later (2013) another inventory took place on the study site. The four years period was selected to eliminate some trees, which can establish unviable sprouts unable to survive longer than one year. Only the sprouts that survived the four-year period were considered to be live (sprouting) and the remaining were considered as dead. Each stump was marked with sheet metal tag with his unique number. The last inventory relevant to this thesis was carried out in 2015. The data collected in the 2009, 2013 and 2015 inventories were used and considered essential for this thesis.

4.2 Data collection

The fundamental operations of this thesis were in-situ field data collections carried out in the years of 2013 and 2015. Abundance of sprouts and their dimensional (dendrometric) characteristics were measured within these inventories. In 2013, each stump of the previously pre-harvest measured trees (2863 in total) was located and checked to determine whether it had resprouted or not, once again with the use of the

Field-map technology (IFER, Ltd., Jílové u Prahy, Czech Republic). Only stumps, which successfully resprouted, were measured. Most sprouts grew directly from the stump or the stump collar. Specific dendrometric measurements of sprouts took place on a set of 5 tallest sprouts per stump. Basal diameter (BD) was measured for each sprout. The measurement was not performed directly on the sprout base since sprouts are significantly thicker in place of their connection to the stump but took place 5 cm above its base. The height of the highest sprout (HS) was also measured. The tallest sprout was used because it is typically considered to be a good predictor of the total sprout biomass of multi-sprout trees (Matula *et al.* 2015) and also because it can be used for calculation of post-harvest competition. The diameters were measured in two perpendicular directions, and the final diameter was defined as the average of these two diameters. Calibrated digital callipers ABS SOMET with a precision of ± 0.1 mm were used for the measurements of diameters. Exactly the same procedures were performed at the second post-harvest inventory in 2015.

4.3 Data analysis

The total data package analysed consisted of datasets from pre-harvest inventory (2009) and post-harvest inventories (2013 and 2015). The dataset is unique, capturing the development of sprouts during six vegetation seasons. It was necessary to calculate the total sprout biomass per stump and increment at first. Appropriate species-specific allometric equations were used to calculate sprout biomass production and increment from the 2013 and 2015 inventories where the value of basal diameter was used as the parameter. The exponential formula used for calculation of biomass was (Matula *et al.* 2015):

$$y = ae^{bx}$$

where:

y is the response variable (biomass in this case)

x is the average value of the given parameter (basal diameter)

a, b are the model coefficients

Own, unique species-specific model coefficients were used for each species (*Quercus*, *Tilia*, *Carpinus*) (Matula *et al.* 2015). Individual sprout biomass for calculation of total biomass per stump (5 from each stump) was summarized. Relative sprout increment was also calculated since biomass was calculated for both inventories (2013 and 2015).

Distance-dependent tree-level Hegyi competition index (Hegyi 1974) was chosen to analyse competition of mutual relations. Hegyi competition index is an individual index using spatial dependence. The formula of the distance-dependent tree-level Hegyi competition index is as follows (Biging, Dobbertin, 1995):

$$CI_{Hegyi} = \sum_{j=1}^{n} \frac{P_j}{P_i(l_{ij}+1)}$$

Where:

 P_i is a parameter of a individual tree (i) as DBH, crown length or height of the highest sprout (HS).

 P_j is a parameter of a competitor tree (j) of the same composition as above (DBH, HS, etc.).

 l_{ij} is the distance between target tree (i) and competitor tree (j).

n is the number of trees in target radius (10 and 5 meters).

The crown length parameter was calculated as the difference between the total tree height and the height of the base of the live crown. Two radiuses of interest (10-meter radius and 5-meter radius) were chosen for precise analysis of competition. The 10-meter radius was chosen because it is considered to be an area, which host the most intensive interaction between the competitors. The smaller, 5-meter radius was subsequently chosen, because the sprouts could be too small to compete with other sprouts located at a distance greater than 5 meters. It has to be pointed out that only trees located in distance grater or equal to 10 meters from the TARMAG II plot boundaries were included in the competition index calculations. Hegyi competition index was used to analyse the competition effect and to create models (Table 3). Preharvest competition was calculated with the use of DBH and length of live crown and post-harvest competition was calculated with the use of height of the highest sprout.

These variables were used for the estimation of pre-harvest crowding (Competition), pre-harvest shading (Competition L) and post-harvest shading (Competition S). Calculations of allometric equations, sprout biomass production and increment were performed in Microsoft Exel.

Generalized linear models (GLM) with gamma distribution (log likelihood) were used to determine whether the pre-harvest crowding, pre-harvest shading or post-harvest shading had an effect on sprout biomass production and increment. The explanatory variables, which were entered to the models were as follows (Table 1): Competition (for 10 and 5 meter radius), Competition L (for 10 and 5 meter radius), Competition S (for 10 and 5 meter radius), Trees (number of surrounding trees in 10-meter radius), SD (standards in 10-meter radius), biomass (g) and increment (g). Only three species (*Tilia*, *Carpinus* and *Quercus*) were abundant enough in the experimental plot to be used in the data analysis. Other species such as *Larix*, *Pinus*, etc. did not resprout, as expected, at all and the *Sorbus* and *Acer* species were not distributed on the plot in numbers, which can be used in statistics. Statistical significance of models was tested using P-values and deviance explained (pseudo \mathbb{R}^2 coefficient of determination; Heinzel 2003). Deviance explained (\mathbb{D}^2) was calculated for all generalized linear models. The simplify equation for deviance explained (\mathbb{D}^2) was used as follows (Faraway 2006):

$1 - \frac{\text{Residual Deviance}}{\textit{Null Deviance}}$

Residual deviance and null deviance were calculated in the GLM model. The null deviance shows how well is the response predicted by the model with nothing but an intercept and the residual deviance shows how well is the response predicted by the model when the predictors are included. The D^2 coefficient describes what proportion of the total variability in the dependent variable was the model able to explain (Faraway 2006). The coefficient values ranges from 0 to 1. The higher the number, the better model is found. In case where the D^2 coefficient was greater than 0.05 statistical significance was demonstrated. The P-value hypothesis test was performed to determine the significance of results. A small P-value (typically 0.05) indicates strong level of significance, so the null hypothesis can be reject. On the other hand when the P-value is larger than given value (typically > 0.05) insignificance is indicated and the null hypothesis is fail to reject (Bayarri 2000).

The probability of resprouting was tested by using generalized linear models (GLM) with a binomial error distribution. The binary response variable was determined according to whether the individual tree resprouted (1) or did not (0). The explanatory variables, which were entered in the models, were as follows (Table 4): DBH (diameter at breast height), height, crown length, trees (number of standing trees in the 10 m or 5 m radius around each tree) and both pre-harvest competitions (Competition, Competition L) at both radiuses (5 m and 10 m). Statistical significance of models was also tested by using the deviance explained (D²). The P-value was also used for the determination of the resulting significance. Only the *Quercus* was abundant enough in the experimental plot to be used in the data analysis.

All models and analyses were performed in the R2.12.0 statistical environment (R Development Core Team 2010). The ggplot2 package (Wickham 2009) was used for visualization and graph creation. All results were plotted in graphs.

5 RESULTS

Overall 2437 stumps of seven tree species (*Acer*, *Carpinus*, *Quercus*, *Larix*, *Pinus*, *Sorbus*, *Tilia*) were measured at the area of interest in Sob šice. Only three species (*Carpinus*, *Quercus* and *Tilia*) had sufficient number of trees for statistical analysis. 1653 stumps sprouted and the other 784 were classified as "dead".

5.1 Effect of competition on biomass production and increment

1054 measured stumps classified as sprouting were used for analyses of competition on biomass production and sprout increment. From which, 1020 are *Quercus*, other 24 were *Carpinus* and last 10 belonged to the genus *Tilia*. Characteristic of the measured dataset are shown in Table 3.

Only four models in total proved any significant interaction between competition and biomass production or sprout increment. Tilia did not show any effect between competitions (pre-harvest crowding, pre-harvest shading and post-harvest shading) and biomass or increment. In the case of Quercus, only post-harvest shading (sprout competition calculated with height of the highest sprout) was significant and showed that it negatively affected the biomass production and increment in both tested radiuses (5 m and 10 m). The models (Figure 8, 9, 14, 15) demonstrate that with an increasing post-harvest shading the biomass production or increment decreases. Result of Carpinus showed that only sprout increment was affected by pre-harvest crowding (competition calculated with DBH) in the 10-meter radius and by pre-harvest shading (competition calculated with length of live crown) in the lower 5-meter radius. The models (Figure 10, 13) show that with increasing pre-harvest crowding (competition calculated with DBH in 10 m radius) and shading (competition calculated with length of live crown in 5 m radius), the increment of sprouts declines. Number of surrounding trees (Figure 16, 17) did not affect the growth of sprouts (in terms of biomass and increment). Post harvest residual trees (standards) negatively affected *Quercus* and *Carpinus* sprout biomass production, where with increasing number of standards, the biomass production decreased.

Table 3 Data summary distributed according species

			Curpu	curping op.					
Trees (r=10m)	Competition (r=10m)	Competition (r=10m) Competition L (r=10m) Competition S	Competition S (r=10m)	Competition (r=5m)	Competition L (r=5m) Competition S (r=5m)	Competition S (r=5m)	Increment (g)	Biomass (g)	SD (r=10m)
17.000	2.826	0.942	0.558	1.410	0.436	0.322	11.990	555.000	0.000
22.000	10.752	4.046	2.521	4.567	2.161	1.281	2910.260	5529.000	3.000
22.300	9.788	4.427	2.801	5.147	2.183	1.370	5583.590	8005.000	3.348
30,000	19.374	6.399	6.445	14.848	3.756	3.052	25709.180	27846.000	7.000
			Tilio	Tilia Sp.					
Trees (r=10m)	Competition (r=10m)	Competition (r=10m) Competition L (r=10m) Competition S	Competition S (r=10m)	Competition (r=5m)	Competition L (r=5m)	Competition S (r=5m)	Increment (g)	Biomass (g)	SD (r=10m)
15.000	4.707	2.432	0.835	2.403	1.093	0.447	700.700	2867.000	0.000
21.000	7.629	4.390	1.887	4.263	2.320	0.957	6032.500	9401.000	4.000
19.700	7.935	5.136	2.711	4.595	3.087	2.026	8116.000	10704.000	3.800
22.000	11.645	9.223	6.412	7.653	6.972	5.822	24880.900	24542.000	7.000
			Querc	Quercus Sp.					
Trees (r=10m)	Competition (r=10m)	Competition (r=10m) Competition L (r=10m) Competition S	Competition S (r=10m)	Competition (r=5m)	Competition L (r=5m) Competition S (r=5m)	Competition S (r=5m)	Increment (g)	Biomass (g)	SD (r=10m)
11.000	0.991	0.001	0.249	0.072	0.001	0.001	12.630	501.600	0.000
22.000	4.177	4.162	2.486	1.845	1.773	1.036	4343.070	5670.200	3.000
22.360	5.228	5.381	3.107	2.316	2.396	1.399	8586.450	10035.200	3.167
42.000	22.725	61.261	27.937	21.004	25.908	17.043	70686.950	74580.700	000.6

Trees (r=10m) = Number of surrounding trees in 10 meter radius (Pre-harvest).

Competition (r=10m) = Pre-harvest competition, calculated by using Hedgy competition index, with surrounding trees in 10 meter radius.

Competition L (r=10m) = Pre-harvest competition (Hedgy competition index) with surrounding trees in 10 meter radius, calculated with length of live crown.

Competition S (=10m) = Post-harvest competition (Hedgy competition index) with surrounding trees in 10 meter radius, calculated with height of the highest sprout.

Increment (g) = Absolute increment of biomass in grams, between years 2013-2015.

Biomass (g) = Calculated weight of woody biomass, by using allometric equations, according to Matula et al. 2015.

SD (r=10m) = Number of standards in 10 meter radius (Post-harvest).

5.1.1 Effect of competition on biomass production

The pre-harvest tree competition calculated with DBH in a 10-meter radius did not affect sprout biomass production after 5 years of growth ($D^2 = 0.07$; P > 0.05 for *Tilia*: P > 0.05; $D^2 = 0.03$ for *Quercus* and for *Carpinus*: P > 0.05; $D^2 = 0.07$, Figure 4). The lowest measured deviance explained was for *Quercus* species. The other two species had slightly higher deviance explained, however their P-values were higher than significance level = 0.05 so the effect was not significant.

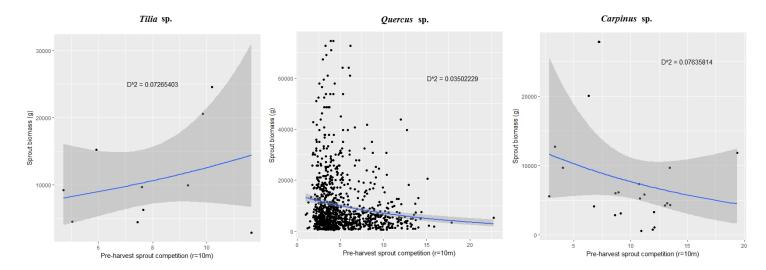


Figure 4 The relationship between pre-harvest tree competition calculated with DBH in 10-meter radius and sprout biomass production 5 years after harvesting. The blue line shows the predicted relationship from the generalised linear model using gamma distribution with log likelihood. The points represent individual observations

Figure 5 displays that competition calculated with DBH for the smaller radius (5 meters) did not affect sprout biomass production after 5 years of growth either. Deviance explained was very small for all three species and P-values were higher than the significance level = 0.05. For *Tilia* were $D^2 = 0.01$; P > 0.05, for *Quercus*: $D^2 = 0.03$; P > 0.05 and for *Carpinus*: $D^2 = 0.04$; P > 0.05.

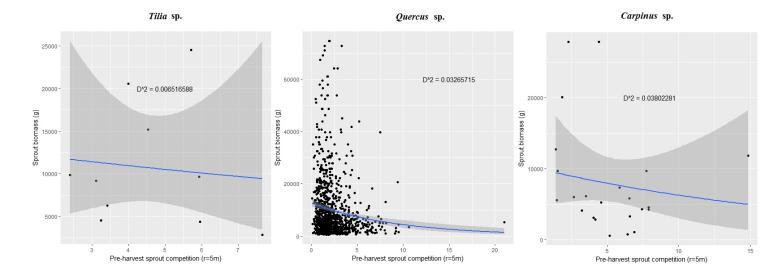


Figure 5 The relationship between pre-harvest tree competition calculated with DBH in 5-meter radius and sprout biomass production 5 years after harvesting. The blue line shows the predicted relationship from the generalised linear model using gamma distribution with log likelihood. The points represent individual observations

Very similar results were discovered for the relationship between pre-harvest tree competition with surrounding trees in 10-meter radius. It was calculated with length of live crown and sprout biomass production 5 years after harvesting (Figure 6). The deviance explained was also very low (for *Tilia* $D^2 = 0.000001$; P > 0.05, for *Quercus* $D^2 = 0.04$; P > 0.05; for *Carpinus*; $D^2 = 0.02$; P > 0.05). It is evident that also the pre-harvest competition with surrounding trees in 10 meter radius, calculated with length of live crown did not have an effect on the biomass production.

Neither the model of pre-harvest tree competition encompassing half radius (5 meters) calculated with length of live crown was significant (Figure 7). The value of deviance explained for *Tilia* was not large ($D^2 = 0.05$) and the P-value was not significant (P > 0.486). Similarly, *Carpinus* D^2 value was slightly higher ($D^2 = 0.06$), which could indicate some relationship between competition and biomass, but P-value was also very high (P = 0.217). Insignificant interaction was also discovered at *Quercus* data where: $D^2 = 0.03$ and P > 0.05.

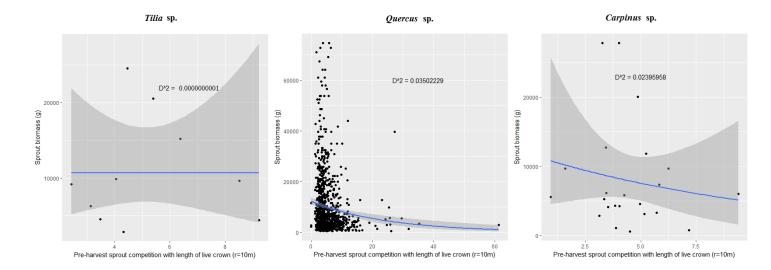


Figure 6 The Relationship between pre harvest tree competition with surrounding trees in 10-meter radius, calculated with length of live crown and sprout biomass production 5 years after harvesting. The blue line shows the predicted relationship from the generalised linear model using gamma distribution with log likelihood. The points represent individual observations

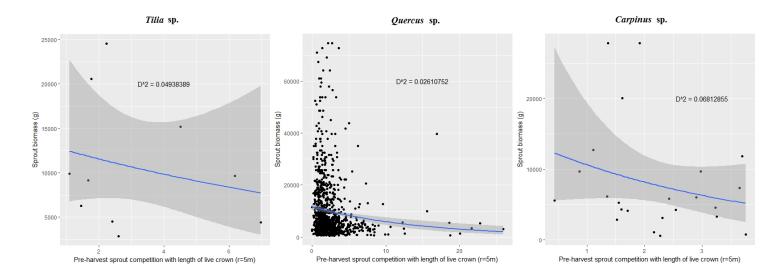


Figure 7 The Relationship between pre-harvest tree competition with surrounding trees in 5-meter radius, calculated with length of live crown and sprout biomass production 5 years after harvesting. The blue line shows the predicted relationship from the generalised linear model using gamma distribution with log likelihood. The points represent individual observations

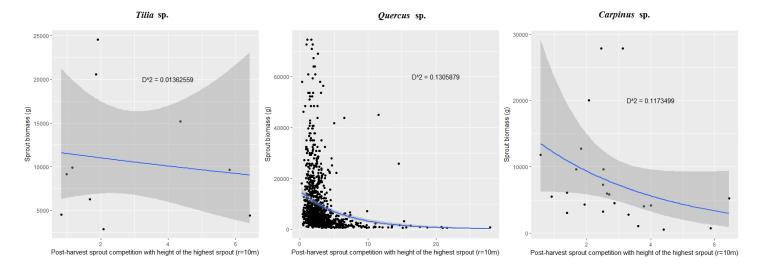


Figure 8 The relationship between post-harvest (3 years) sprout competition with surrounding stumps in 10-meter radius, calculated with height of the highest sprout and sprout biomass production 5 years after harvesting. The blue line shows the predicted relationship from the generalised linear model using gamma distribution with log likelihood. The points represent individual observations

The Figure 8 shows that post-harvest (3 years) sprout competition with surrounding stumps in 10-meters radius, calculated with height of the highest sprout is affected only in *Quercus* sprout biomass production 5 years after harvesting where the deviance explained for *Quercus* is $D^2 = 0.13$ and indicates strong linear relationship between biomass and competition. The P-value was highly significant (P = 0.00001). As it can be seen in Figure 5 in case of *Quercus*, the smaller is post-harvest competition the greater is the increase of the sprout biomass. *Carpinus* with $D^2 = 0.12$ also indicates strong relationship but its P-value (P= 0.101) is insignificant so in this case competition did not affect significantly the biomass production. *Tilia* had both of the values insignificant ($D^2 = 0.03$ and P > 0.05).

In 5-meter radius it was also only sprout biomass production of *Quercus* that was affected by post-harvest (3 years) sprout competition, in the same way (with increasing post-harvest competition, biomass decreased). The deviance explained was still high with $D^2 = 0.08$ and the P-value was significant (P = 0.00001) as well. As shown in Figure 9 the other two species were not affected by sprout competition in term of biomass. The results measured for *Tilia* are $D^2 = 0.02$; P > 0.05 and for *Carpinus* $D^2 = 0.01$; P > 0.05.

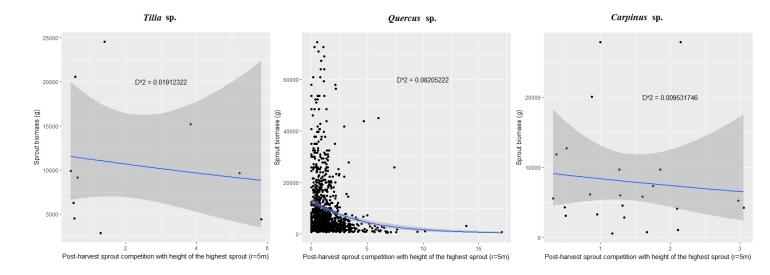


Figure 9 The relationship between post-harvest (3 years) sprout competition with surrounding stumps in 5-meter radius, calculated with height of the highest sprout and sprout biomass production 5 years after harvesting. The blue line shows the predicted relationship from the generalised linear model using gamma distribution with log likelihood. The points represent individual observations

5.1.2 Effect of competition on increment

The results show that only increment of *Carpinus* was significantly affected by pre-harvest competition (calculated with DBH) in 10-meter radius. As shown in Figure 10 the deviance explained indicated strong relationship between the competition and the sprout increment for *Carpinus* and *Tilia* species, but only in case of *Carpinus* the P-value was significant. The model predicts that with the increasing pre-harvest competition (calculated with DBH), the sprout increment declines. The statistical indices for *Carpinus* were $D^2 = 0.11$; P = 0.0167 and for *Tilia* were $D^2 = 0.20$; P > 0.05. The data for *Quercus* did not indicate any relationship. The deviance explained was $D^2 = 0.03$ and P > 0.05.

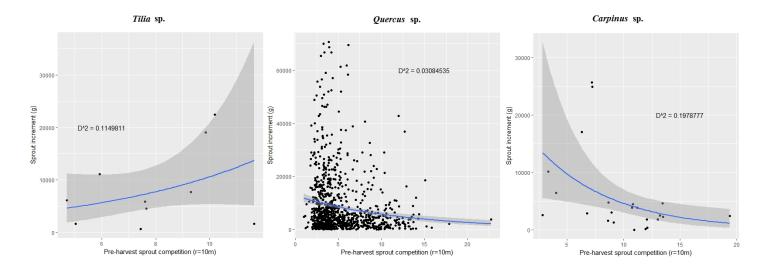


Figure 10 The relationship between pre-harvest tree competition in 10-meter radius, calculated with DBH and sprout increment. The blue line shows the predicted relationship from the generalised linear model using gamma distribution with log likelihood. The points represent individual observations

In the 5-meter radius (Figure 11), the deviance explained also indicated strong relationship between the pre-harvest competition and the increment in case of *Carpinus*, but the P-value was insignificat. The *Carpinus* values were $D^2 = 0.15$ and P > 0.05. Its relationship with increment for the two other species (*Quercus* and *Tilia*) was not affected by pre-harvest competition. The statistical P-value and D^2 values were insignificant for both *Tilia* ($D^2 = 0.01$; P > 0.05) and *Quercus* ($D^2 = 0.03$; P > 0.05).

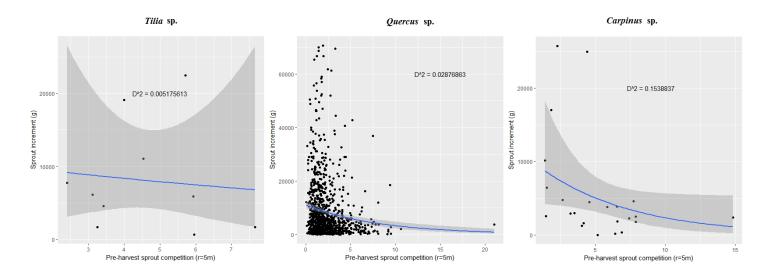


Figure 11 The relationship between pre-harvest tree competition in 5-meter radius, calculated with DBH and sprout increment. The blue line shows the predicted relationship from the generalised linear model using gamma distribution with log likelihood. The points represent individual observations

Figure 12 shows that the relationship between pre-harvest competition, calculated with length of live corwn in 10-meter radius did not affect the sprout increment in all tree species (*Tilia*, *Quercus* and *Carpinus*). Both deviance explained and P-value were insignificant and did not show any relationship. The values here were: for *Tilia*: $D^2 = 0.01$; P > 0.05, for *Quercus*: $D^2 = 0.02$; P > 0.05 and for *Carpinus*: $D^2 = 0.03$, P > 0.05.

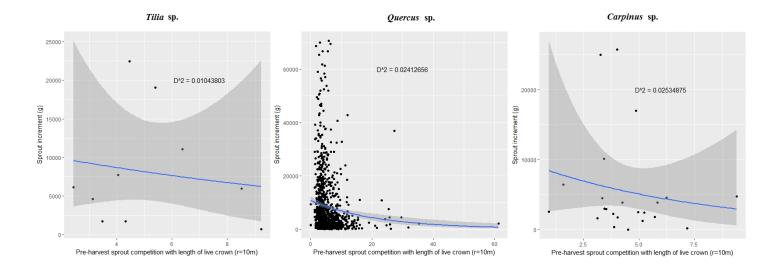


Figure 12 The Relationship between pre-harvest tree competition with surrounding trees in 10-meter radius, calculated with length of live crown and sprout increment. The blue line shows the predicted relationship from the generalised linear model using gamma distribution with log likelihood. The points represent individual observations

However, when we lowered the interest area of competition by half to five meter radius, as shown in Figure 13, it becomes obvious that there was a statisticly significant relationship between pre-harvest competition (calculated with length of live crown) and increment at *Carpinus* ($D^2 = 0.07$; P = 0.0307). The model predicted, that with a increasing pre-harvest competition, increment decreases. The results for other two species (*Quercus* and *Tilia*) were insignificant. *Tilia* values were: $D^2 = 0.01$; P > 0.05 and *Quercus* values: $D^2 = 0.02$; P > 0.05

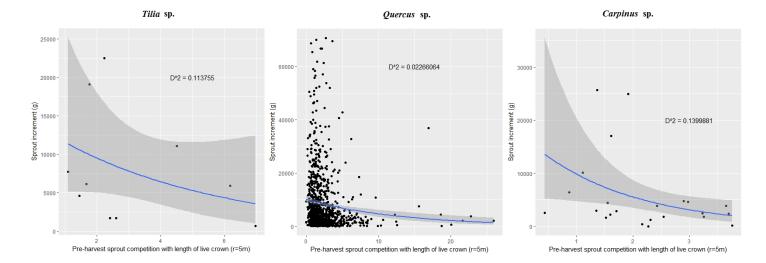


Figure 13 The Relationship between pre-harvest tree competition with surrounding trees in 5-meter radius, calculated with length of live crown and sprout increment. The blue line shows the predicted relationship from the generalised linear model using gamma distribution with log likelihood. The points represent individual observations

According to Figure 14 only *Quercus* indicated relationship between the post-harvest competition with surrounding trees in 10-meter radius (calculated with height of the highest sprout) and the increment. With an increasing post-harvest competition, increment decreased. The *Quercus* deviance explained indicated strong linear relationship ($D^2 = 0.10$) and the P-value supported this model with strong significance level, which was approaching to 0 (P = 0.000002). On the contrary, other two species (*Tilia* and *Carpinus*) did not show any particular relationship between the post-harvest competition and the increment. *Tilia*'s deviance explained was on the edge of significancy ($D^2 = 0.05$) and could indicate some relationship, however the P-value was strongly insignificant (P > 0.05). The values for *Carpinus* were: $D^2 = 0.03$ and P > 0.05.

The same results are visible in Figure 15 where competition radius was lowered to 5-meter radius. Relationship between post-harvest competition (calculated with height of the highest sprout) and increment was proved by the model only in case of *Quercus*. The deviance explained for *Quercus* was $D^2 = 0.03$ and also the P-value was significant P < 0.05. For *Carpinus* and *Tilia* the model did not suggest any relationship. The values were insignificant for both (*Carpinus*: $D^2 = 0.01$; P > 0.05 and for *Tilia*: $D^2 = 0.01$; P > 0.05).

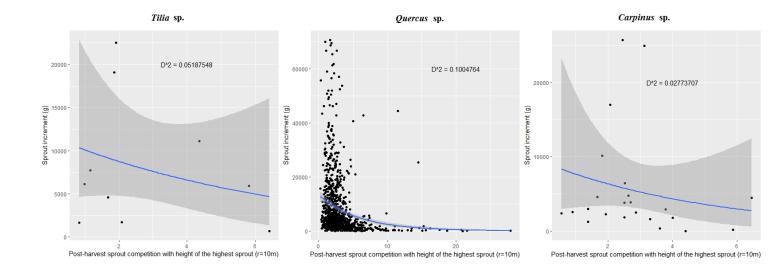


Figure 14 The relationship between post-harvest (3 years) sprout competition with surrounding stumps in 10-meter radius, calculated with height of the highest sprout and sprout increment. The blue line shows the predicted relationship from the generalised linear model using gamma distribution with log likelihood. The points represent individual observations

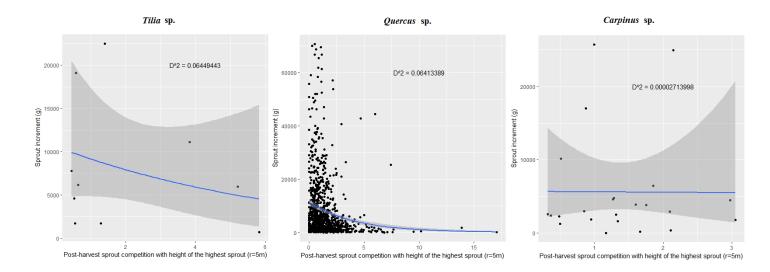


Figure 15 The relationship between post-harvest (3 years) sprout competition with surrounding stumps in 5-meter radius, calculated with height of the highest sprout and sprout increment. The blue line shows the predicted relationship from the generalised linear model using gamma distribution with log likelihood. The points represent individual observations

5.1.3 Effect of surrounding trees to increment and biomass production

The number of surrounding trees in 10-meter radius did not affect the biomass production of all three species. However in the case of *Tilia*, as shown in Figure 16, strong linear relationship according to deviance explained ($D^2 = 0.29$) existed, but at the same time the P-value was insignificant (P = 0.7). Therefore, the model could not prove an existing statistically significant relationship between the number of surrounding trees and the biomass production after 5 years. It was also insignificant for the other two species (*Carpinus*: $D^2 = 0.01$; P > 0.05 and *Quercus*: $D^2 = 0.03$; P > 0.05).

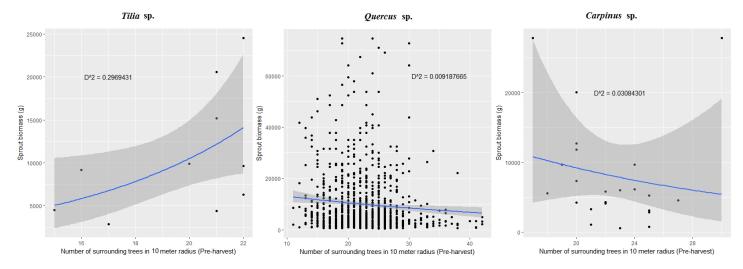


Figure 16 The relationship between number of the surrounding trees (10-meter radius) and sprout biomass production 5 years after harvesting. The blue line shows the predicted relationship from the generalised linear model using gamma distribution with log likelihood. The points represent individual observations

As in the previous figure, Figure 17 indicates that, there was a strong relationship between the numbers of surrounding trees in 10-meter radius and the increment in the case of *Tilia* and also of *Carpinus*. However, the insignificance of P-value rejected the relationship in both cases. The values measured for *Tilia* are $D^2 = 0.26$; P > 0.05 and for *Carpinus*: $D^2 = 0.17$; P > 0.05. Values of *Quercus* did not indicate any relationship between the increment and the number of surrounding trees where the deviance explained was very low ($D^2 = 0.01$) and the P-value also insignificant (P > 0.05).

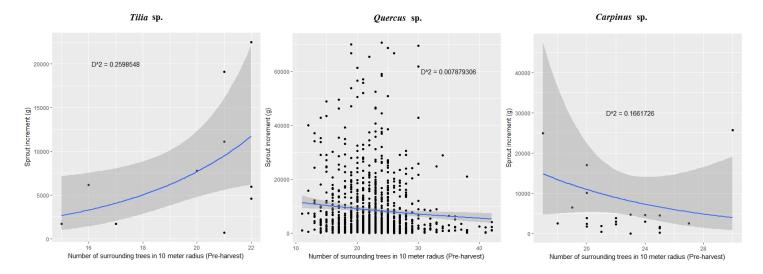


Figure 17 The relationship between number of the surrounding trees (10-meter radius) and sprout increment. The blue line shows the predicted relationship from the generalised linear model using gamma distribution with log likelihood. The points represent individual observations

5.1.4 Effect of standards to sprout biomass production

The number of post-harvest standards significantly negatively affected the sprout biomass production of *Quercus* and *Carpinus*. The models of Figure 18 show that with increasing numbers of standards in the 10-meter radius, the sprout biomass decreased. The measured deviance explained of *Quercus* was $D^2 = 0.14$ and the P-value was P < 0.05. *Carpinus* values were both also significant (D2 = 0.36 and P = 0.002). In case of *Tilia* the deviance explained indicated strong significance (D2 = 0.24) but the P-value was strongly insignificant (P = 0.2) so the model could not prove the relationship between the number of standards and the biomass production.

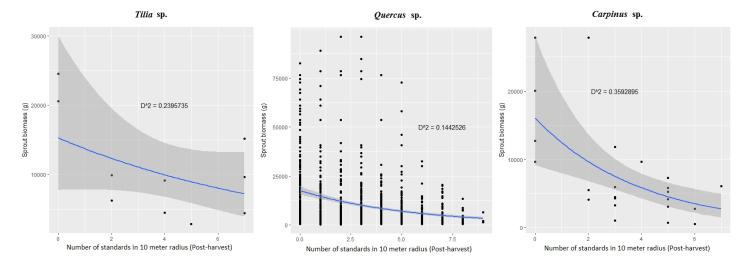


Figure 18 The relationship between number of the standards (10-meter radius) and sprout biomass 5 years after harvesting. The blue line shows the predicted relationship from the generalised linear model using gamma distribution with log likelihood. The points represent individual observations

5.2 Resprouting ability

Data from all 2437 measured stumps (sprouting and death) were used in this analysis but only the Quercus genus was suitable for this analysis. *Tilia* successfully resprouted on every measured stump (10 stumps were observed at the area). It can, therefore, be noted that its resprouting ability in the area of Sob šice was 100%. Carpinus resprouting ability was also very high, from 26 observations 24 stumps successfully resprouted. Only 2 stumps did not and were classified as dead. Carpinus resprouting success at the Sob šice area was 92,3%. Tilia and Carpinus were not suitable for the resprouting ability analysis because of such small data set. Additional species observed at the target area were not also suitable for this analysis. Some did not sprout at all (*Pinus* sp., *Larix* sp.) and some like *Sorbus* sp. occurred in the area only in very few numbers so it was not statistically possible to work with them. Summary of used data is shown in Table 4.

The most significant was the relationship between the resprouting ability and the pre-harvest DBH. As shown in Figure 19, the model clearly indicates that with the increasing DBH, resprouting ability decreased. Deviance explained for this model was relatively significant ($D^2 = 0.06$) and the Pvalue also proved strong significance (P = 0.0001). The same result occurred in the case of pre-harvest tree height. The model (Figure 19) shows, that with increasing pre-harvest tree height, the probability of sprouting decreased. The deviance explained for height was on the edge of significance $(D^2 = 0.05)$. The P-value, on the other hand was strongly significant (P = 0.0001). According to the models the preharvest shading and crowding did not affect the resprouting ability at all (Figure 22, 23).

 Table 4 Resprouting ability data summary

'	DBH (mm)	Height (m)	OBH (mm) Height (m) Crown_Length (m) Trees ((r=10m)	Trees (r=5m)	Competition (r=10m)	Competition (r=5m)	Trees (r=5m) Competition (r=10m) Competition (r=5m) Competition L (r=10) (Competition L (r=5)
Min.	70.000	2.200	0.200	000.9	1.000	0.709	0.012	0.441	0.011
Median	213.000	16.420	4.190	21.000	5.000	3.965	1.801	4.104	1.816
Mean	206.000	15.320	4.492	21.480	5.187	4.831	2.292	5.073	2.383
Max.	462.000	24.050	16.600	43.000	16.000	069:09	53.780	61.260	38.180
7-000 (m-	5.10m) = Mm	there of custom	Trace ((10) - Muchae of mountains team in § (10) mater and in	motor modine					

I rees (r=5;10m) = Number of surrounding trees in 5 (10) meter radius.

Competition L (r=5;10m) = Pre-harvest competition (Hedgy competition index) with surrounding trees in 5 (10) meter radius, calculated with length of live crown.

Competition (r=5;10m) = Pre-harvest competition, calculated by using Hedgy competition index, with surrounding trees in 5 (10) meter radius.

- 39 -

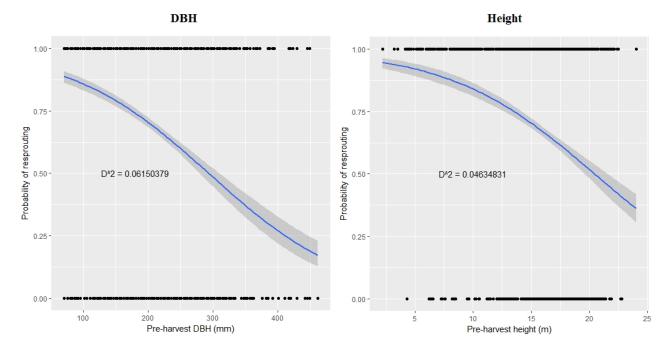


Figure 19 Relationship between probability of resprouting and pre-harvest DBH; height. The blue line shows the predicted relationship from the generalised linear model using a binomial error distribution. The points represent individual observations

It can be observed at Figure 20 that pre-harvest crown length did not affect the probability of sprouting. Model suggested that the probability of resprouting decreased with an increase in crown length. But both deviance explained ($D^2 = 0.002$) and P-value (P > 0.05) were insignificant.

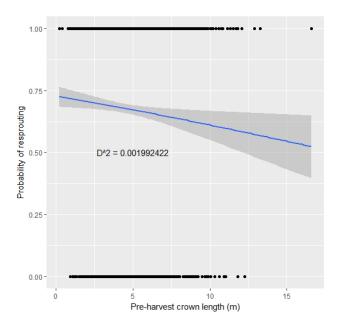


Figure 20 Relationship between probability of resprouting and pre-harvest crown length. The blue line shows the predicted relationship from the generalised linear model using a binomial error distribution. The points represent individual observations

According to Figure 21 the number of surrounding trees did not affect the resprouting ability. The model did not prove any relationship even with the radius lowered down to 5 meters. The deviance explained was insignificant for both radiuses (5 and 10 meters). The values for 10-meter radius were: $D^2 = 0.002$ and for 5 meter radius: $D^2 = 0.002$. The P-value was also insignificant for both (P > 0.05).

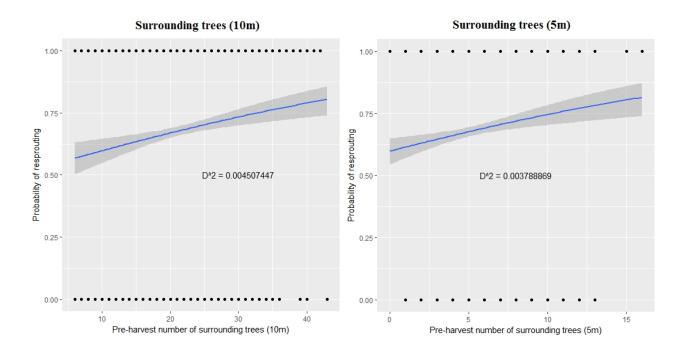


Figure 21 Relationship between probability of resprouting and pre-harvest number of surrounding trees in-10 meter radius and 5-meter radius. The blue line shows the predicted relationship from the generalised linear model using a binomial error distribution. The points represent individual observations

Pre-harvest competition, calculated with DBH did not affect the probability of resprouting in the case of 10-meter radius (Figure 22). The deviance explained for the 10 meters radius was slightly under the edge of significance ($D^2 = 0.04$). The P-value on the other hand was insignificant (P > 0.05). In the case of half radius (5 meter) model did not show any effect between the pre-harvest competition and the probability of resprouting. The deviance explained ($D^2 = 0.04$) and P-value (P > 0.05) were both insignificant.

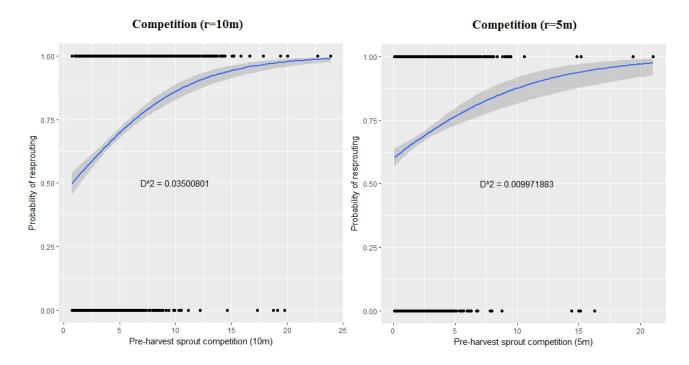


Figure 22 Relationship between probability of resprouting and pre-harvest competition, calculated with DBH in 10-meter radius and 5-meter radius. The blue line shows the predicted relationship from the generalised linear model using a binomial error distribution. The points represent individual observations

The last relationship tested was between the pre-harvest competition, calculated with length of live crown and the probability of resprouting. According to Figure 23 there was no such relationship and the competition did not affect the probability of resprouting. The deviance explained and the P-value were strongly insignificant in both cases (10 and 5 meter radius). The values for the 10-meter radius were $D^2 = 0.002$; P > 0.05 and for the 5-meter radius were $D^2 = 0.002$; P > 0.05.

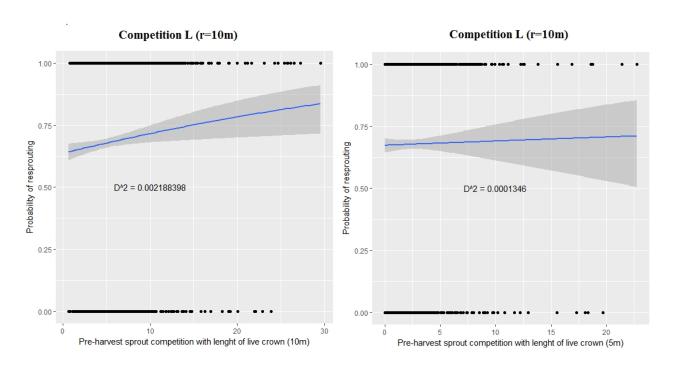


Figure 23 Relationship between probability of resprouting and pre-harvest competition, calculated with length of live crown in 10-meter radius and 5-meter radius. The blue line shows the predicted relationship from the generalised linear model using a binomial error distribution. The points represent individual observations

6 DISSCUSION

Sprouts and the resprouting ability of trees were used for centuries as natural regeneration of forest stands after natural outbreaks (Helle 1999, Tredici 2001, Johnson 2002) or anthropologically to manage systematically restored coppice forest (Bu ek 2010). Nowadays, there is strong increase of interest in sprouts and resprouting ability to restore the old coppice forests from economical perspective in the sense of sprout biomass as a source of renewable energy (Hall 2002). But very little is known about the influence of competition on spouts and resprouting ability of temperate trees. From that point of view the main goal of this thesis was to find any existing relationships between competition and sprout growth or resprouting ability of temperate trees in TARMAG II (Sob šice) experimental plot. This thesis showed that pre-harvest and post-harvest competition can significantly affect the sprout growth, but can differ between individual species and by the effect on the growth. The results clearly show that the pre-harvest competition did not affect the *Quercus* resprouting ability.

Sprout growth

To discover whether the pre-harvest shading, pre-harvest crowding or post-harvest shading has an effect on sprout growth of temperate trees, the three main temperate tree species were tested: *Quercus petraea*, *Tilia cordata* and *Carpinus betulus*.

The results showed that **pre-harvest crowding** (competition calculated with DBH) did not affect sprout growth in terms of biomass and affects only *Carpinus* in the 10-meter radius in terms of increment. *Tilia* and *Quercus* were not affected by pre-harvest crowding. This is an interesting result, because an increase in stem competition (crowding) from neighbouring trees usually decreases nutrient availability for trees, which in turn increases accumulation of carbohydrates in the root mass and that can lead to sprout growth boost (Kabeya, Sakai 2005). Model (Figure 10) showed that increased pre-harvest crowding decreased the amount of increment of *Carpinus*. This phenomenon of *Carpinus* could be explained by the fact that decreased availability of nutrients and water (by crowding) increased accumulation of carbohydrates in the *Carpinus* root mass, which could than initiate strong sprout growth and resprouting ability (Matula *et al.* 2012), but on the other hand, the lack of available nutrients and water caused by pre-harvest crowding simply cannot supply the sprouts growth

afterwards, which could cause that increment was decreased. Therefore, since there is no such effect of *Carpinus* to pre-harvest crowding described in literature I suppose that this effect can be caused by small *Carpinus* dataset and that could lead to false statistical significance of the model.

The pre-harvest shading (calculated with length of live crown) also only affected the sprout growth of *Carpinus* (Figure 13). Unlike the other species (*Tilia* and *Quercus*) *Carpinus* was negatively affected not only by pre-harvest crowding (10-meter radius) but also by crown competition (pre-harvest shading in the-5 meter radius) in terms of sprout increment. According to Kabey, Sakai (2005) increased light availability increases the level of stored carbohydrates. Therefore, a decrease in carbohydrate storage associated with a decrease in light availability of the pre-harvest trees could negatively affect the future sprout growth. Results corroborate this suggestion only in the case of *Carpinus* increment and only at the narrowest radius of 5 meters. But as previously mentioned this could be a result of false statistical significance of a small data set. Though, as results show the sprout growth of *Carpinus* (in terms of increment) are affected by pre-harvest competition (crowding and shading) and the sprout growth (neither the biomass or increment) of *Tilia* and *Quercus* were not.

Since the original hypothesis was that increasing pre-harvest competition (crowding, shading) will negatively affect growth of sprouts of temperate trees, due to decreased nutrient and carbohydrate reserves from pre-harvest (Kabeya, Sakai 2005), the results of this thesis did not prove the hypothesis. Sprout increment was negatively affected by pre-harvest competition (shading and crowding) only in the case of Carpinus, which could be caused by false statistical significance of Carpinus model due to small data set of Carpinus (24 individuals). Another possible explanation could be that rich mesic soils of TARMAG II site can easily supply the sprouts with nutrients, thus the pre-harvest crowding did not affect sprout growth afterwards.

The results clearly showed that **post-harvest shading** (competition calculated with height of the highest sprout) had a significantly negative effect on sprout growth of *Quercus petraea* (both biomass and increment). Increasing post-harvest shading leads to decreasing the sprout growth of *Quercus* (Figure 8, 9, 14, 15). This is very important and interesting conclusion, which can be affirmed by the studies of Coates *et al.* (2009)

and Kabeya, Sakai (2005) whose result also showed that increasing shading negatively affected growth of shade intolerant trees. The results of this thesis, similarly to Johnson et al. (2002), showed that the growth of oak sprouts is negatively affected by shading. The explanation to why *Quercus* was negatively affected by post-harvest shading and *Tilia* and *Carpinus* were not is probably simple: *Quercus* is shade intolerant (light demanding) species even at early stages of growth (Johnson et al. 2002). The initial growth of sprouts is high to help the tree persist and quickly recover from the intervention or outbreak by using of carbohydrate reserves in belowground organs (Bond, Midgley 2001). But as observed from the results this initial high growth can lead to creation of early crown competition (shading) among sprouts. As *Quercus* is the only shade intolerant specie (tested in this thesis) its growth (biomass and increment) is suppressed by crown competition (shading) of surrounding sprouts in both tested radiuses (5 and 10 meter). By contrast, the growth of shade tolerant species of Tilia and Carpinus was not affected by post-harvest competition. This is very important because it indicates that shade tolerant species can easily overcome and suppressed the cooccurring shade intolerant species after harvest and shift forest composition towards a long-term dominance of shade-tolerant species, as described by Johnson et al. (2002) on the examples of oak forests in the USA. Relative abundance of shade-tolerant species was also evident in TARMAG II experimental plot where 96% of all species was Quercus. This suggestion is also supported by Matula et al. (2012) whose results showed that shade tolerant species are better resprouters and can suppress and overcome shade intolerant species like Quercus. Hence the results are important for managing future establishments of coppice forests and for re-coppicing old forest in the Czech Republic or Europe because many of the potential stands are dominated or codominated by *Quercus petraea* (Poleno 1994). Pruning, thinning and negative selection of the less economically valuable co-occurring tree species could lower the impact of competition (shading) on shade intolerant species like Quercus and boost their growth. However, additional management practices could be costly and they could lead to economic unprofitability.

Number of surrounding trees was also taken into consideration. The results showed that surrounding trees did not affect the sprout growth of temperate trees in term of biomass or increment. This is also interesting because initial suggestion was: that higher numbers of surrounding pre-harvest trees can negatively affect sprout growth.

On the other hand the post-harvest **number of standards** significantly affected the sprout biomass production of Quercus and Carpinus (Figure 18). This is probably because of the shade-intolerance of Quercus. The increasing numbers of standards probably create an effect of shading, which can negatively affect the sprout growth of shade intolerant species. Tilia, as shade tolerant species, can support this suggestion because it was not affected by the amount of post-harvest standards. This hypothesis corroborates with Kabeya, Sakai (2005) whose result showed that increased shading negatively affect growth of shade intolerant trees. Also Johnson et al. (2002) showed that *Quercus* as shade intolerant (light demanding) species was negatively influenced by shading. However, Carpinus which is shade tolerant species, was also negatively affected by increasing numbers of standards. It should not be affected according to previous suggestions made. Therefore the reaction of Carpinus is unclear. It seems that increasing numbers of post-harvest standards can also create competition for nutrients and water, which can have an effect on Carpinus. As it is a shade tolerant species it is more likely to be negatively affected in terms of competition for nutrients and water (crowding), subsequently by competition for light (shading). It could also be that the negative reaction of Carpinus to numbers of standards was caused by false statistical significance of the model, due to small amount of Carpinus data set.

Resprouting ability

Only *Quercus*, among all species found on TARMAG II experimental plot, was statistically suitable for the creation of binomial models in which initial hypothesis was tested. The effects of pre-harvest tree characteristic and pre-harvest competition on resprouting ability were tested here. Used variables were: size parameters of the parent tree such as diameter at breast height (DBH), total tree height and crown length, and pre-harvest competitions such as crowding and shading. According to the results DBH and height of the parent tree had the most significant effect on the resprouting ability of Quercus in TARAMAG II research plot (Figure 19). Specifically, the bigger was the DBH and the tree height of the parent tree, the smaller was the ability to resprout. Tree height and DBH are considered to be in strong correlation with age of the tree (Matula et al. 2012, Johnson et al. 2002). So the results of this thesis are in agreement with the study of Tredici (2001) and Johnson et al. (2002) who discovered that resprouting ability declines with increasing age of the parent tree. But it is evident that the influence of age on resprouting ability can be species specific, because in contrast to Quercus, almost every stump of Tilia and Carpinus across all the ages classes and diameters, resprouted. Possible explanation of this theory can be attributed to bark thickness. Johnson et al. (2002) found that with increasing age and DBH the bark thickness (physical resistance) also increases. So that tree species with a thin and soft bark like Tilia and Carpinus can easily resprout in older ages and tree species like Quercus with thicker and harder to penetrate bark could have considerable difficulties to resprout (Matula et al. 2012).

In contrast to initial hypothesis, which assumed that pre-harvest crowding and pre-harvest shading does affect the probability of sprouting of *Quercus*, the results showed that competition did not affect the resprouting ability of *Quercus* at all (Figure 22, 23). This is interesting for coppice forestry and re-coppicing of old stands, because it shows that shaded and crowded stands do not have an effect on the resprouting ability of *Quercus* after harvest.

Tilia successfully resprouted from every measured stump. *Tilia* proved to be the most successful resprouter (best sprouter) on the site. This finding corroborates with the works of Matula *et al.* (2012) and Piggot (1989) who both proved a very high sprouting ability of *Tilia cordata*. Also almost every individual of *Carpinus* resprouted. As both

species are shade tolerant, and successfully resprout on almost every stump, we can say that resprouting ability of shade tolerant temperate tree species is very high or that shade tolerant species are better resprouters than shade-intolerant species of temperate trees. This suggestion can be confirmed by the study of Everham, Brokaw (1996), who also observed that shade-tolerant species resprout with greater frequency than shade-intolerant species. Given the results we can assume that resprouting ability have implications in forest composition because better resprouters, such as the shade-tolerant species (*Tilia* and *Carpinus*) in TARMAG II site, could easily outcompete poorer resprouters as *Quercus* and thus shift the future forest composition.

Implications for coppice management

The negative effect of post-harvest competition of the sprouts growth in *Quercus*, the most valuable species in terms of wood value, suggests that some level of thinning to support this species and to suppress better sprouting of less valuable species can be recommended. The thinning should therefore focus on the removal of sprouts of *Tilia* and *Carpinus* in the neighbourhood of resprouting oaks, which may limit oak growth, thus decrease the value of wood produced.

7 SUMMARY

Resprouting and sprout growth are life strategies and key traits of persistence of trees. Together with competition they are crucial and critical to the development and sustainable management of coppice forests. Very little is known about the influence of competition on spout growth and resprouting ability of temperate trees although it is crucial for developing optimal silvicultural measures for coppice management. Therefore, the main aim of this diploma thesis was to statistically analyse the effect of competition on resprouting success and sprout growth of temperate trees. The unique dataset, capturing the development of sprouts from harvest through six vegetation seasons, were measured by Field-map technology within three inventories (2009, 2013) and 2015) at the TARMAG II (Sob šice) experimental plot. Species-specific allometric equations and distance-dependent tree-level Hegyi competition index were used for the calculation of sprout biomass, the increment and the competition analysis of mutual interactions. An effect of pre-harvest crowding, pre-harvest shading or post-harvest shading on sprout biomass production and increment was tested through the use of generalized linear models (GLM) with gamma distribution (log likelihood). Probability of resprouting was tested through utilizing generalized linear models with a binomial error distribution. According to the results the pre-harvest competition (crowding, shading) did not affect sprout growth of *Quercus* and *Tilia*, but it negatively affected the increment of Carpinus by pre-harvest competition (shading in the 5-meter radius and crowding in the 10-meter radius). Additionally, the post-harvest shading showed a significantly negative effect on sprout growth of *Quercus* (both biomass and increment). The number of standards also negatively affected sprout biomass production of *Quercus* and Carpinus. The pre-harvest shading and crowding did not affect the resprouting ability of Quercus. DBH and height of the parent tree had the most significant effect on the resprouting ability of *Quercus petraea*, where the higher was the DBH and the tree height was, the lower was the resprouting ability. It can be noted that the results are important for future management and establishment of coppice forests or for recoppicing of old forest in Europe. The results indicate that there is a significant crown competition (shading) among sprouts in early stages of growth, which negatively affects sprout biomass production and increment. Also, that pre-harvest competition does not affect the resprouting ability of temperate trees. Due to significant post-harvest competition, appropriate management practises (like thinning) should be applied in the future. There is a lack of empiric information for sustainable management of coppice and restored coppice forest. Further research on this topic is needed.

8 SHRNUTÍ

R st výmladk a výmladná schopnost strom jsou strategie a klí ové vlastnosti pro persistenci strom . Spolu s kompeticí jsou d ležité pro vývoj a udržitelné hospoda ení s výmladkovými lesy. Stále toho moc nevíme o vlivu kompetice na r st výmladk a na výmladnou schopnost strom mírného pásma, i když tato informace je klí ová pro vývoj optimálního managementu pro pa eziny. Z toho d vodu bylo hlavním cílem této diplomové práce statisticky analyzovat vliv kompetice na výmladnou schopnost a r st výmladk . Unikátní soubor dat, zachycující r st výmladk od t žby p es 6 vegeta ních sezón, byl nam en pomocí technologie Filed-map b hem t í inventarizací (v letech 2009, 2013, 2015). M ení a sb r dat byl provád n na výzkumné ploše TARMAG II (Sob šice). Alometrické rovnice a Hegyiho kompeti ní index byly použity pro výpo ty biomasy a p ír st výmladk a k analyzování konkuren ních vztah . Ke zjišt ní, kde m ly p ed-t žební kompetice a po-t žební kompetice vliv na p ír st a biomasu výmladk , byly použity generalizované lineární modely s gamma rozd lením. Výmladná schopnost strom byla testována pomocí generalizovaných lineárních model s binomickým rozd lením. Dle výsledk p ed-t žební kompetice o sv tlo (shading) a kompetice o vodu a živiny (crowding) neovlivnila r st výmladk lípy malolisté a dubu zimního, ovlivn n byl pouze p ír st u habru. Na druhou stranu pot žební kompetice o sv tlo významn negativn ovlivnila r st výmladk u dubu zimního. P ed-t žební kompetice o sv tlo a kompetice o vodu a živiny neovlivnila výmladnou schopnost dubu. Nejvýznamn jší vliv na výmladnou schopnost dubu m la výška a tlouš ka (DBH) mate ného stromu, kde se zvyšující se výškou a tlouš kou se výmladná schopnost dubu snižovala. Výsledky této práce jsou d ležité pro hospoda ení a budoucí zakládání výmladkových les v Evrop, protože ukazují, že i velmi brzo po t žb se u výmladk významn projevuje negativní vliv kompetice (o sv tlo) na p ír st a r st výmladk . Také, že p ed-t žební kompetice (o sv tlo, o vodu a živiny) neovlivní výmladnou schopnost strom po t žb . Z d vodu významné kompetice (o sv tlo) mezi výmladky po t žb by bylo do budoucna vhodné aplikovat výchovné zásahy, nap íklad probírky. Nicmén, protože je stále málo empirických dat pro udržitelné hospoda ení ve výmladkových lesích, je zapot ebí dalších výzkum a m ení na toto téma.

9 REFERENCES

Bayarri, M. J., Berger, J. O. (2000). "P-values for composite null models [with discussion]," J. Amer. Statist. Assoc. 95, 1127

Biging, G. S., Dobbertin, M. (1995). Evaluation of Competition Indices in Individual Tree Growth Models. Forest Science, 41, 360-377.

Bond, W. J., Midgley, J. J. (2001). Ecology of sprouting in woody plants: The persistence niche. Trends Ecol. Evol., 16, 45-51.

Bu ek, A. (2010). Význam starobylých výmladkových les v kulturní krajin eské republiky. In: Fórum o krajin a workshop management kulturní krajiny. Sb. p ísp. ZF MENDELU v Brn . CD. 7s.

Burkhard, H. E., Tomé M. (2012). Modeling forest trees and stands. New York: Springer, c2012. ISBN 978-94-007-1597-4.

Clements, F. E., Shelford, V. E. (1939). Bio-ecology. New York: John Wiley & Sons. 425s.

Coates, K. D., Canham, C. D. & LePage, P. T. (2009). Above versus below ground competitive effects and responses of a guild of temperate tree species. Journal of Ecology, 97, 118-130.

Culek, M. *et al.* (2005). Biogeografické len ní eské republiky II. díl. AOPK R, Praha.

Everham, E. M. & Brokaw, N. V. (1996). Forest damage and recovery from catastrophic wind. The Botanical Review, 62, 113-185.

Faraway, J. J. (2006). Extending the linear model with R: generalized linear, mixed effects and nonparametric regression models. Boca Raton, Fla.: Chapman & Hall/CRC, 2006. Texts in statistical science series. ISBN 1-58488-424-X. pp 59.

FIELDMAP. [online]. 2017 [cit. 2017-03-11]. Dostupné z: http://www.fieldmap.cz/

Grime, J. P. (2001). Plant strategies, vegetation processes, and ecosystem properties. 2nd ed. Chichester, John Wiley & Sons Ltd.

Hall, J.P. (2002). Sustainable production of forest biomass for energy. Forest. Chron. 78, 391–396.

Hallé, F. (1999). Ecology of reiteration in tropical trees. Pp. 93-107 in M. H. Kurmann & A. R. Hemsley (eds.), The evolution of plant architecture. Roy. Bot. Gard., Kew, London.

Harper, J. L. (1977). Population biology of plants. Academic Press, London.

Hegyi, F. (1974). A simulation model for managing jack-pine stands. Growth models for tree and stand simulation (ed F. J.), pp. 74-90. Royal College of Forestry, Stockholm.

Heinzl, H. and Mittlböck, M. (2003). Pseudo R-squared measures for Poisson regression models with over- or underdispersion. Computational Statistics and Data Analysis, V44, 253-271.

Hodgkinson, K. C. (1998). Sprouting success of shrubs after fire: height-dependent relationships for different strategies. Oecologia, 115, 64-72.

Jeník, J., Pavliš J. (2011). Terestrické biomy: lesy a bezlesí Zem . Brno: Mendelova univerzita v Brn , 2011. ISBN 978-80-7375-481-5.

Johnson, P. S., Shifley S. R., Rogers R. (2002) The ecology and silviculture of oaks. New York: CABI, c2002. p. 100-103.

Kabeya, D., Sakai, S. (2005). The relative importance of carbohydrate and nitrogen for the resprouting ability of Quercus crispula seedlings. Annals of Botany, 96, 479-488.

Kadavý, J., Kneifl M., Servus, M. *et al.* (2011). Nízký a st ední les - plnohodnotná alternativa hospoda ení malých a st edních vlastník lesa. Mendel University in Brno, Brno. 83 p.

Kadavý, J., Kneifl M., Knot R. (2010). Nízký a st ední les: Založení experimentální plochy nízkého a st edního lesa projektu TARMAG na území ŠLP Masaryk v les K tiny (TARMAG II - Sob šice) [online] citation made on 7. March 2017. Available at:http://www.nizkyles.cz/content/view/94/91/lang,czech1250//.

Kadavý, J., Kneifl M., Knot R. (2009). Nízký a st ední les: Založení experimentální plochy nízkého a st edního lesa projektu TARMAG na území ŠLP Masaryk v les K tiny [online] citation made on 12. March 2017. Available at www: < http://www.nizkyles.cz/content/view/82/91/lang,czech1250/>.

Liming, F.G. (1942). Blackjack oak in the Missouri Ozarks. Journal of Forestry 40, 249–252.

Mad ra, P., Martínková, M. (2009). Role vegetativní regenerace a propagace d evin v p irozených podmínkách R. In: Dreslerová, J., Svátek, M. (eds.) (2009): Sborník p ísp vk ze seminá e Nízké a st ední lesy v krajin , Brno, 3.–4. dubna 2009. MZLU v Brn . CD. 6 s.

Matula, R., Svátek, M., K rová, J., Úradní ek, L., Kadavý, J. & Kneifl, M. (2012). The sprouting ability of the main tree species in Central European coppices: implications for coppice restoration. European Journal of Forest Research, 131, 1501-1511.

Matula, R., Svátek, M. & epka, R. (2014). The effect of fire exclusion on the structure and tree mortality patterns of a caldén (Prosopis caldenia Burkart) woodland in semi-arid Central Argentina. Journal of Arid Environments, 100–101, 72-77.

Morav ík, P. (1993). Indexy kompetice a jejich korelace s tlouš kovým p ír stem ve smrkovém porostu. Zprávy lesnického výzkumu. Svazek XXXVIII, . 2/1993. 41 – 45s.

Munro, D. D. (1974). Forest growth models---a prognosis. P. 7-21 in Growth models for tree and stand simulation, J. Fries (ed.). Royal Coil. For., Res. Notes 30, Stockholm

Mze. (1995). Lesnický nau ný slovník. 2. díl O – . Praha: Ministerstvo zem d lství. 683s.

Nagelkerke N. J. D. (1991). A note on a general definition of the coefficient of determination. Biometrika 78(3):691

Ng, F. S. P. (1999). The development of the tree trunk in relation to apical dominance and other shoot organizational concepts. J. Trop. Forest Sci. 11: 270-285.

Polanský, B., et al. (1956). P st ní les III. díl. Praha: SZN.

Poleno, Z. (1994). Lesnický slovník nau ný I. Praha: Ministerstvo zem d lství v Agrospoji.

Poleno, Z. Vacek, S., Podrázský V., (2011). P stování les . 2., upr. a dopl. vyd. Kostelec nad ernými lesy: Lesnická práce, 319 s. ISBN 978-80-87154-99-1.

Pigott C. D. (1989) Factors controlling the distribution of Tilia cordata Mill at the northern limits of its geographical range. New Phytol 112(1):117–121. doi:10.1111/j.1469-8137.1989.tb00316.x

R Development Core Team (2010) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Slavíková, J. (1986). Ekologie rostlin. 1. vyd. Praha: SPN, 366 s.

Svoboda, P. (1952). Život lesa. Praha: Brázda,

Tolasz, R. A KOL. (2007). Atlas podnebí eska: Climate Atlas of Czechia. 1. vyd. Praha: eský hydrometeorologický ústav,. ISBN 978-80-86690-26-1.

Vogt, A.R. and Cox, G.S. (1970). Evidence for the hormonal control of stump sprouting by oak. Forest Science 16, 165–171.

Wickham H. (2009). ggplot2: elegant graphics for data analysis. Springer, New York

Wilson, J. B. (1988). Shoot competition and root competition. Journal of Applied Ecology, 25, 279-296,

10 LIST OF TABLES AND FIGURES

10.1 List of tables

Table 1 Trees species composition on TARMAG II experimental site before conversion, according to Kadavý *et al.* 2010

Table 2 TARMAG II experimental site characterization according to geomorphologic division of Czech Republic (Culek *et al.* 2005)

Table 3 Data summary distributed according species

Table 4 Resprouting ability data summary

10.2 List of figures

Figure 1 Drawing by Lukáš Patra depicting sprout originate from A stump, B root

Figure 2 TARMAG II felling intensities according to Kadavý *et al.* (2009)

Figure 3 TARMAG II research plot. Data from google maps 2016, adjusted by Lukáš Patra

Figure 4 The relationship between pre-harvest tree competition calculated with DBH in 10 m radius and sprout biomass production 5 years after harvesting.

Figure 5 The relationship between pre-harvest tree competition calculated with DBH in 5 m radius and sprout biomass production 5 years after harvesting.

Figure 6 The Relationship between pre harvest tree competition with surrounding trees in 10 meter radius, calculated with length of live crown and sprout biomass production 5 years after harvesting.

Figure 7 The Relationship between pre-harvest tree competition with surrounding trees in 5 meter radius, calculated with length of live crown and sprout biomass production 5 years after harvesting.

- **Figure 8** The relationship between post-harvest (3 years) sprout competition with surrounding stumps in 10-meter radius, calculated with height of the highest sprout and sprout biomass production 5 years after harvesting.
- **Figure 9** The relationship between post-harvest (3 years) sprout competition with surrounding stumps in 5-meter radius, calculated with height of the highest sprout and sprout biomass production 5 years after harvesting.
- **Figure 10** The relationship between pre-harvest tree competition in 10-meter radius, calculated with DBH and sprout increment.
- **Figure 11** The relationship between pre-harvest tree competition in 5-meter radius, calculated with DBH and sprout increment.
- **Figure 12** The Relationship between pre-harvest tree competition with surrounding trees in 10-meter radius, calculated with length of live crown and sprout increment.
- **Figure 13** The Relationship between pre-harvest tree competition with surrounding trees in 5-meter radius, calculated with length of live crown and sprout increment.
- **Figure 14** The relationship between post-harvest (3 years) sprout competition with surrounding stumps in 10-meter radius, calculated with height of the highest sprout and sprout increment.
- **Figure 15** The relationship between post-harvest (3 years) sprout competition with surrounding stumps in 5-meter radius, calculated with height of the highest sprout and sprout increment.
- **Figure 16** The relationship between number of the surrounding trees (10-meter radius) and sprout biomass production 5 years after harvesting.
- **Figure 17** The relationship between number of the surrounding trees (10-meter radius) and sprout increment.
- **Figure 18** The relationship between number of the standards (10-meter radius) and sprout biomass 5 years after harvesting.
- **Figure 19** Relationship between probability of resprouting and pre-harvest DBH; height.

Figure 20 Relationship between probability of resprouting and pre-harvest crown length.

Figure 21 Relationship between probability of resprouting and pre-harvest number of surrounding trees in 10-meter radius and 5-meter radius.

Figure 22 Relationship between probability of resprouting and pre-harvest competition, calculated with DBH in 10-meter radius and 5-meter radius.

Figure 23 Relationship between probability of resprouting and pre-harvest competition, calculated with length of live crown in 10-meter radius and 5-meter radius.

11 APPENDICES

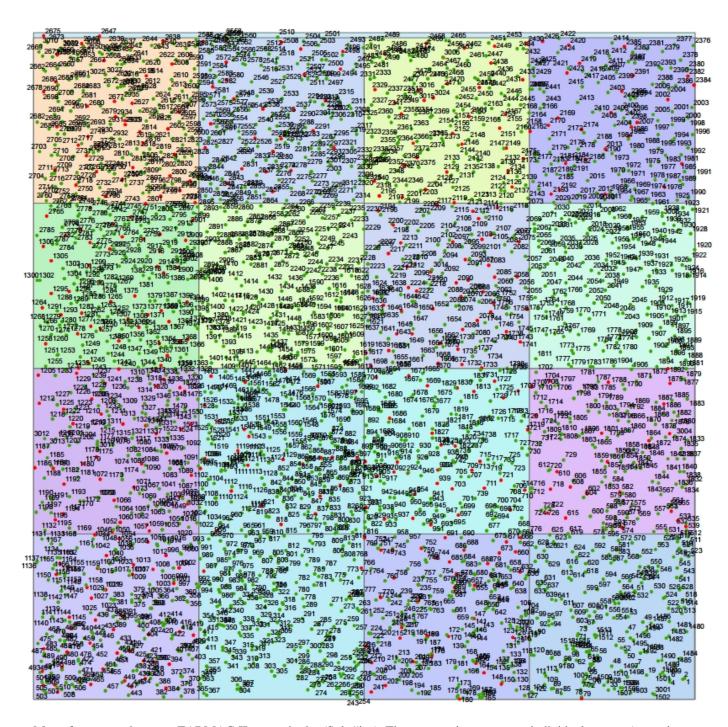
11.1 List of appendices

Appendix 1 TARMAG II map (of stumps and standards)

Appendix 2 Photos of TARMAG II research plot (Sob šice)

Appendix 3 Graph overview

Appendix 2 TARMAG II map



Map of measured trees at TARMAG II research plot (Sob šice). The green points represent individual stumps (sprouting and dead) and red points represent standards. As the source for this map were data from in situ Field-map measurements.

Appendix 3 Photos from TARMAG II research plot



Stump sprouts of *Quercus petraea* at TARMAG II research plot (Sob šice). Author: Lukáš Patra

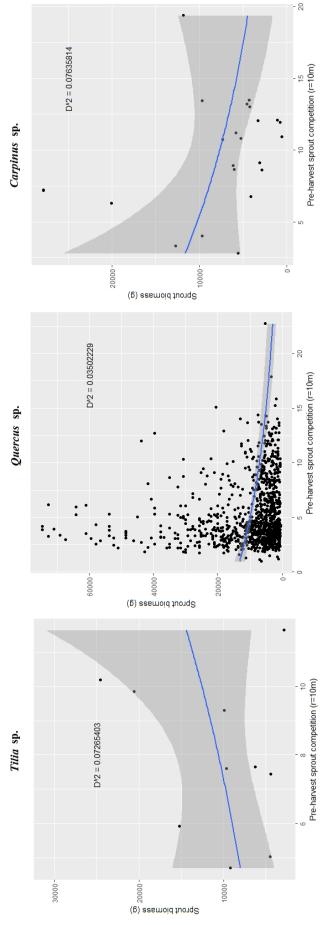


Sheet metal tag with an identification number of tree Author: Lukáš Patra

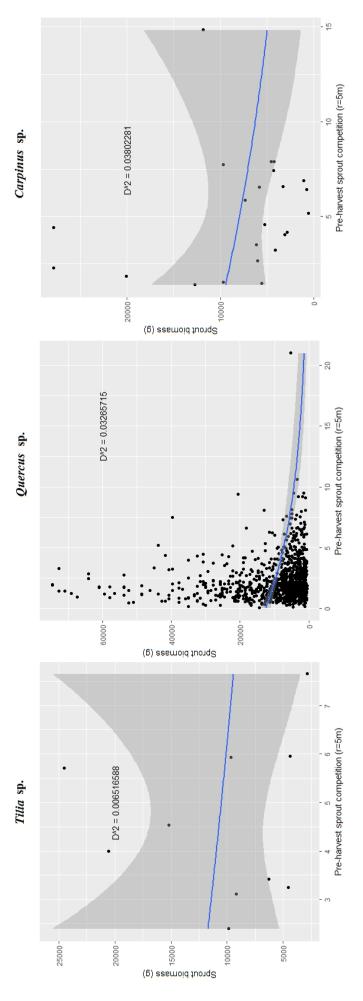


Basal diameter measurement of the sprouts, using a digital caliper Author: Lukáš Patra

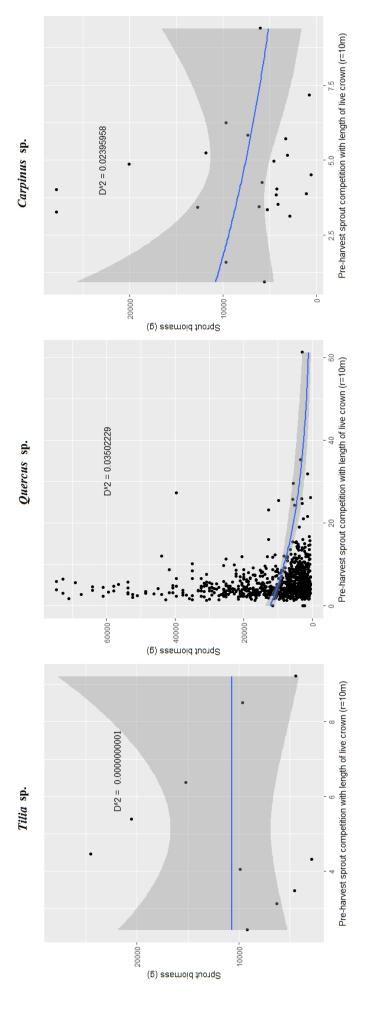
Appendix 3 Graph overview



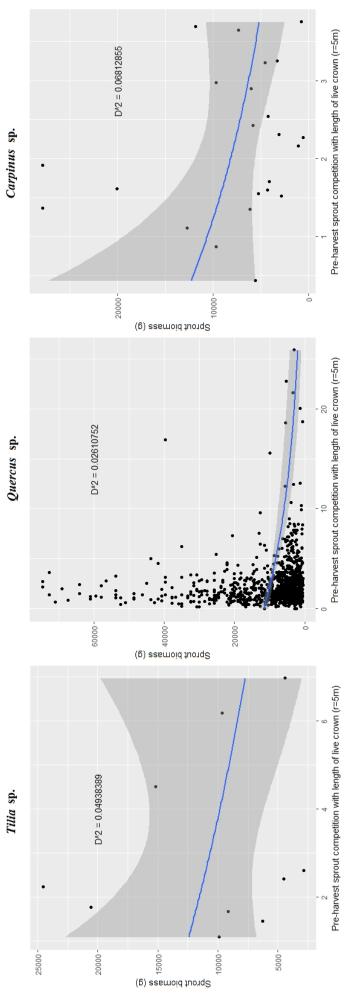
Overview of Figure 4 The relationship between pre-harvest tree competition calculated with DBH in 10-meter radius and sprout biomass production 5 years after harvesting. The blue line shows the predicted relationship from the generalised linear model using gamma distribution with log likelihood. The points represent individual observations



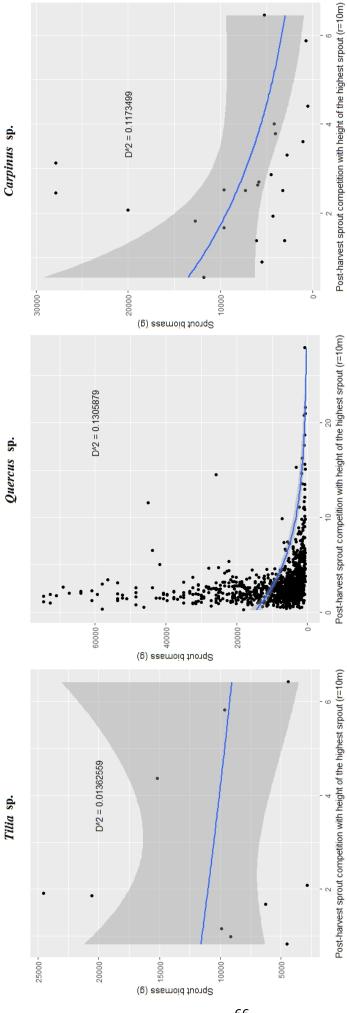
Overview of Figure 5 The relationship between pre-harvest tree competition calculated with DBH in 5-meter radius and sprout biomass production 5 years after harvesting. The blue line shows the predicted relationship from the generalised linear model using gamma distribution with log likelihood. The points represent individual observations



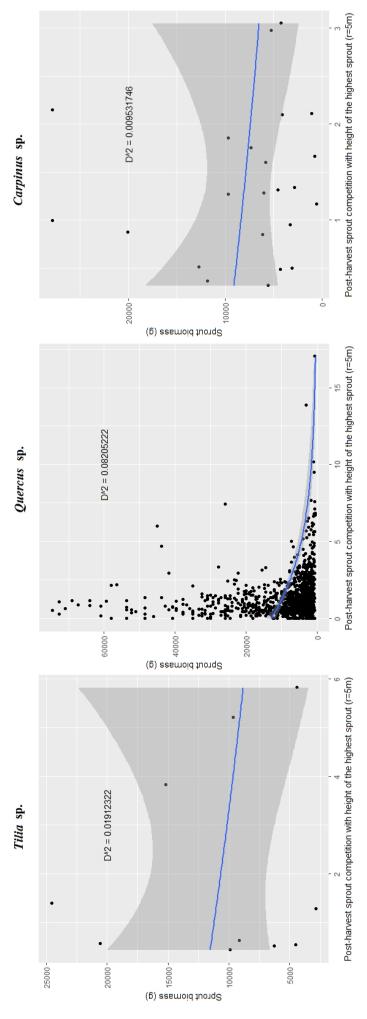
Overview of Figure 6 The Relationship between pre harvest tree competition with surrounding trees in 10-meter radius, calculated with length of live crown and sprout biomass production 5 years after harvesting. The blue line shows the predicted relationship from the generalised linear model using gamma distribution with log likelihood. The points represent individual observations



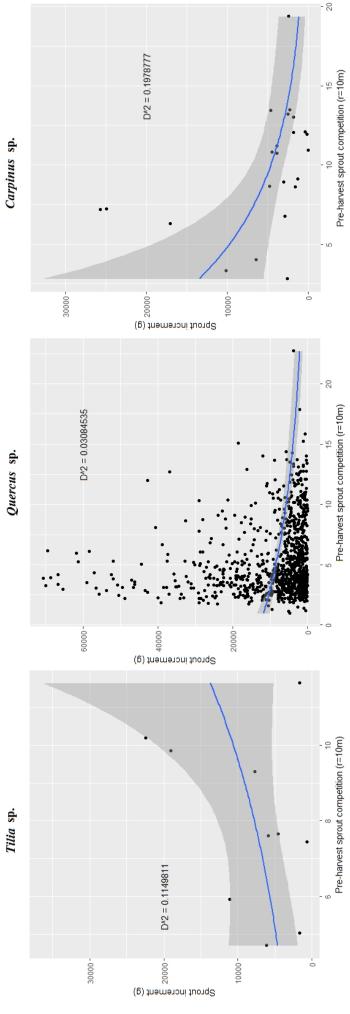
Overview of Figure 7 The Relationship between pre-harvest tree competition with surrounding trees in 5-meter radius, calculated with length of live crown and sprout biomass production 5 years after harvesting. The blue line shows the predicted relationship from the generalised linear model using gamma distribution with log likelihood. The points represent individual observations



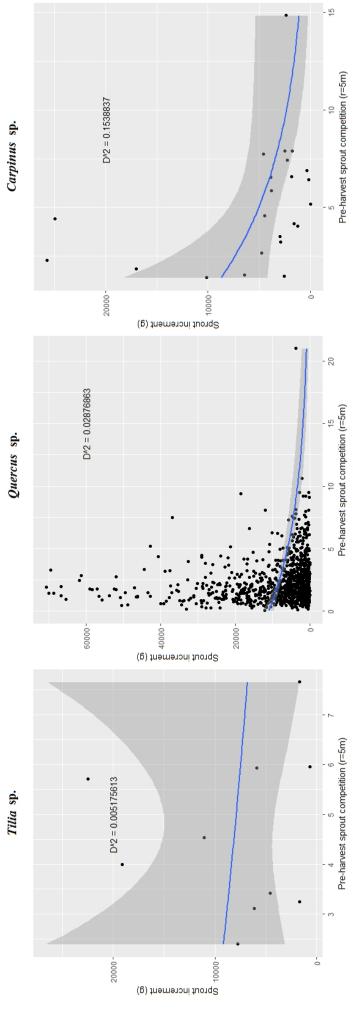
Overview of Figure 8 The relationship between post-harvest (3 years) sprout competition with surrounding stumps in 10-meter radius, calculated with height of the highest sprout and sprout biomass production 5 years after harvesting. The blue line shows the predicted relationship from the generalised linear model using gamma distribution with log likelihood. The points represent individual observations



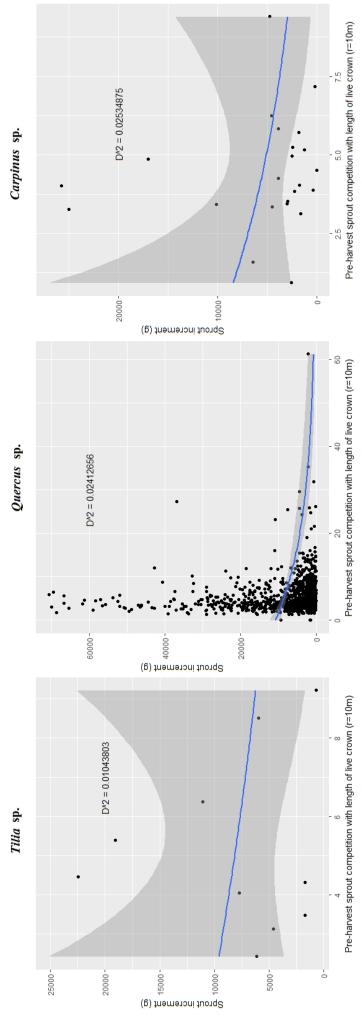
Overview of Figure 9 The relationship between post-harvest (3 years) sprout competition with surrounding stumps in 5-meter radius, calculated with height of the highest sprout and sprout biomass production 5 years after harvesting. The blue line shows the predicted relationship from the generalised linear model using gamma distribution with log likelihood. The points represent individual observations



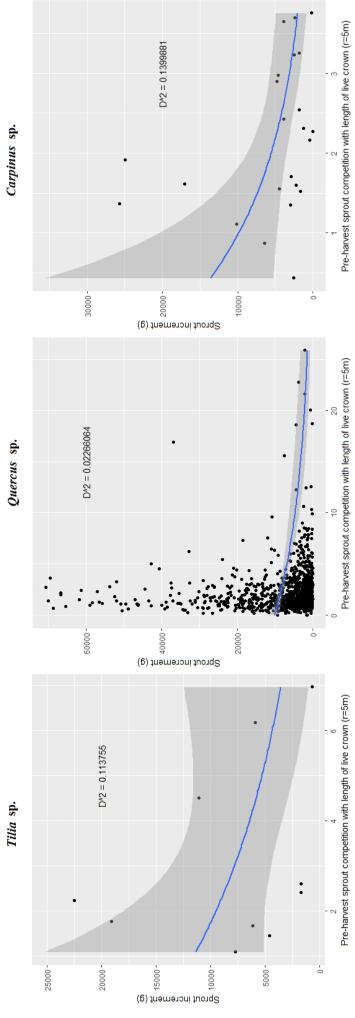
Overview of Figure 10 The relationship between pre-harvest tree competition in 10-meter radius, calculated with DBH and sprout increment. The blue line shows the predicted relationship from the generalised linear model using gamma distribution with log likelihood. The points represent individual observations



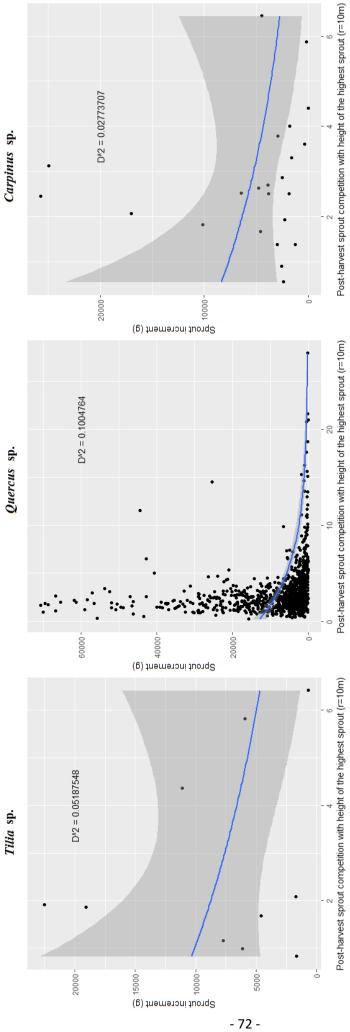
Overview of Figure 11 The relationship between pre-harvest tree competition in 5-meter radius, calculated with DBH and sprout increment. The blue line shows the predicted relationship from the generalised linear model using gamma distribution with log likelihood. The points represent individual observations



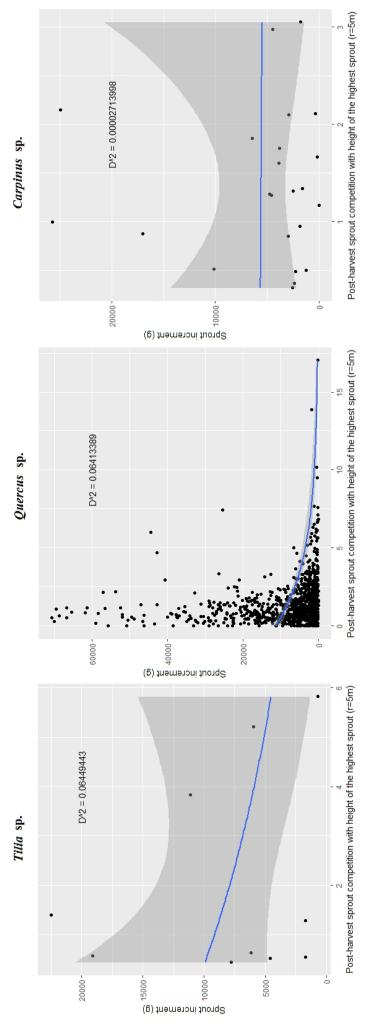
Overview of Figure 12 The Relationship between pre-harvest tree competition with surrounding trees in 10-meter radius, calculated with length of live crown and sprout increment. The blue line shows the predicted relationship from the generalised linear model using gamma distribution with log likelihood. The points represent individual observations



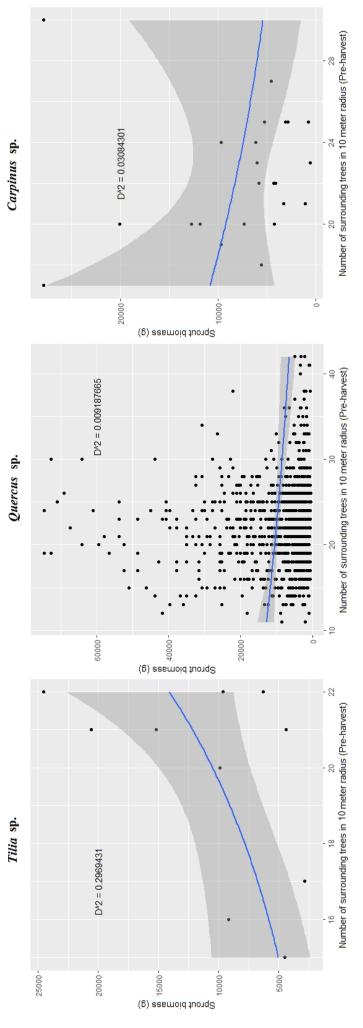
Overview of Figure 13 The Relationship between pre-harvest tree competition with surrounding trees in 5-meter radius, calculated with length of live crown and sprout increment. The blue line shows the predicted relationship from the generalised linear model using gamma distribution with log likelihood. The points represent individual observations



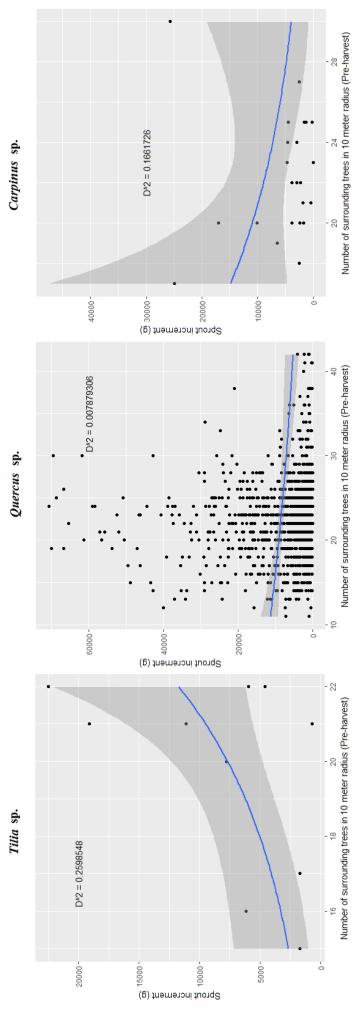
Overview of Figure 14 The relationship between post-harvest (3 years) sprout competition with surrounding stumps in 10-meter radius, calculated with height of the highest sprout and sprout increment. The blue line shows the predicted relationship from the generalised linear model using gamma distribution with log likelihood. The points represent individual observations



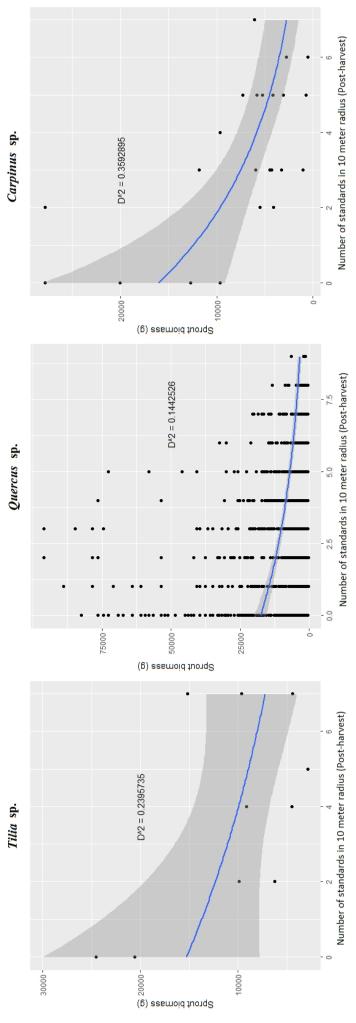
the highest sprout and sprout increment. The blue line shows the predicted relationship from the generalised linear model using gamma distribution with log Overview of Figure 15 The relationship between post-harvest (3 years) sprout competition with surrounding stumps in 5-meter radius, calculated with height of likelihood. The points represent individual observations



Overview of Figure 16 The relationship between number of the surrounding trees (10-meter radius) and sprout biomass production 5 years after harvesting. The blue line shows the predicted relationship from the generalised linear model using gamma distribution with log likelihood. The points represent individual observations



Overview of Figure 17 The relationship between number of the surrounding trees (10-meter radius) and sprout increment. The blue line shows the predicted relationship from the generalised linear model using gamma distribution with log likelihood. The points represent individual observations



Overview of Figure 18 The relationship between number of the standards (10-meter radius) and sprout biomass 5 years after harvesting. The blue line shows the predicted relationship from the generalised linear model using gamma distribution with log likelihood. The points represent individual observations

_	7	7	_