Mendel University in Brno

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DIFFERENCES IN PHOTOSYNTHESIS AND PLANT WATER STATUS BETWEEN COPPICE AND HIGH FOREST

DIPLOMA THESIS

2016/2017 Bc. Marie Matoušková

Zadání práce

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Author: Bc. Marie Matoušková

Title: *Differences in photosynthesis and plant water status between coppice and high forest*

Abstract: This diploma thesis focuses on comparison of photosynthesis and tree water status between high forest and coppice of *Quercus petraea* (Matt.) Liebl. Four different types of management were investigated during vegetation season 2016: high forest, coppice on clear-felled site, coppice with standards and seedlings. Methods of leaf gas exchange and water potential measurements allowed to study transpiration, photosynthesis and its response to light and CO_2 concentration and leaf water potential. All these physiological parameters were studied as linked to weather conditions and various levels of drought stress. When the soil water was not limiting factor trees in all variants of experiment behaved similarly. However, during mild to severe drought stress the coppice was superior to seedlings and to high forest. It showed higher photosynthesis rate (2.49 μmol m^{-2} s^{-1}) than seedlings (0.86 μmol m^{-2} s^{-1}), both under moderate water stress. Coppice also had higher stomatal conductance and quantum yield of fluorescence than high forest which allowed to higher photosynthetic rates. The lowest value of predawn water potential was in high forest (-3.27 MPa) whereas highest in coppice (-2.01 MPa) which indicated better water availability and lower evapotranspiration demands imposed on coppice sprouts due to their lower height and therefore lower overall aerodynamic conductance. Response of net photosynthesis to CO_2 concentration revealed higher carboxylation rates in high forest than in coppice but low stomatal conductance was a reason for overall lower photosynthetic rates in high forest than in coppice. Due to its superiority under water stress coppice forest may be a viable option for forest management on dry sites during the climate change.

Keywords: chlorophyll fluorescence; coppice; coppice with standards; drought stress; high forest; photosynthesis; plant physiology; plant water status; Sessile oak; *Quercus petraea* (Matt.) Liebl.,

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Název: *Rozdíly ve fotosyntéze a vodním provozu mezi nízkým a vysokým lesem*

Abstrakt: Tato diplomová práce se zabývá porovnáním fotosyntézy a vodního provozu vysokého a nízkého lesa. Během vegetační sezóny roku 2016 byly zkoumány tři rozdílné hospodářské způsoby dubu zimního (*Quercus petraea* (Matt.) Liebl.): vysoký les ve dvou růstových stupních: semenáčky v náletu a porost ve stádiu kmenoviny, nízký les a střední les. Na úrovni listu byla studována transpirace, fotosyntéza a její reakce na různé intenzity světla a rozdílnou koncentraci CO_2 a vodní potenciál. Všechny tyto fyziologické parametry byly dány do souvislostí s počasím a různými úrovněmi stresu suchem. Za nelimitujícího obsahu vody v půdě nebyly významné rozdíly mezi jednotlivými variantami experimentu. Avšak nízký les lépe odolával stresu suchem než les vysoký. Za mírného vodního stresu měly výmladky daleko vyšší rychlost fotosyntézy (2.49 μmol m^{-2} s^{-1}) než semenáčky (0.86 μmol m^{-2} s^{-1}). Nízký les prokázal také vyšší stomatální vodivost a kvantový výtěžek fotosyntézy než vysoký les, což mu také umožnilo vyšší rychlost fotosyntézy. Nejnižší hodnota vodního potenciálu před rozbřeskem byla naměřena u vysokého lesa (-3.27 MPa), zatímco nejvyšší byla v nízkém lese (-2.01 MPa), což indikuje lepší přístup k vodě a nižší evapotranspiraci zapříčiněnou pravděpodobně celkově nižší aerodynamickou vodivostí nízkého lesa. Reakce fotosyntézy na změny koncentrací CO_2 odhalila vyšší rychlost karboxylace u vysokého lesa než u nízkého lesa, nicméně jejich nízká stomatální vodivost byla důvodem k celkově nižší rychlosti fotosyntézy, než tomu bylo u nízkého lesa. Schopnost nízkého lesa odolávat suchu jej předurčuje jako možnou alternativu lesního hospodaření na vysychavých lokalitách v procesu globálních klimatických změn.

Klíčová slova: dub zimní; fotosyntéza; fyziologie rostlin; chlorofylová fluorescence; nízký les; střední les; *Quercus petraea* (Matt.) Liebl.; vodní provoz; vodní stres; vysoký les

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List of abbreviations

Ψ_w	Water potential (MPa)
Φ_{PSII}	Quantum yield of photosystem II photochemistry
1B1	Forest type: oak-hornbeam forest with meadow-grass and soft leaved sedge on a plateau and rounded ridges
1C2	Forest type: dry oak-hornbeam forest with meadow-grass
A	(Light saturated) Net assimilation rate (μmol m^{-2} s^{-1})
A_{max}	Maximum assimilation rate (μmol m^{-2} s^{-1})
A_{sat}	CO_2 saturated assimilation rate (μmol m^{-2} s^{-1})
A-C_i curve	CO_2 response curve (also A/C_i curve)
ANOVA	Analysis of variance
CHMI	Czech Hydrometeorological Institute (in Czech Český hydrometeorologický ústav – ČHMÚ)
DBH	Diameter at breast height
E	Transpiration rate (mmol m^{-2} s^{-1})
FAO	Food and Agricultural Organization of the United Nations
F_v/F_m	The quantum efficiency of open photosystem II centres
$F_{v'}/F_{m'}$	The quantum efficiency of closed photosystem II centres
GPS	Global Positioning System
g_b	Leaf boundary-layer conductance (mmol m^{-2} s^{-1})
g_m	Mesophyll conductance (mmol m^{-2} s^{-1})
g_s	Stomatal conductance (mmol m^{-2} s^{-1})
I_{comp}	Light compensation point (mmol (photons) m^{-2} s^{-1})
IGA	Internal Grant Agency

I_{max}	Light saturation point beyond which there is no significant change in A (mmol (photons) m^{-2} s^{-1})
$I_{sat(50)}$	Light saturation point for $A + R_D$ equal to 50% of A_{max} (mmol (photons) m^{-2} s^{-1})
J	Rate of photosynthetic electron transport (µmol m^{-2} s^{-1})
J_{max}	Maximum rate of photosynthetic electron transport (µmol m^{-2} s^{-1}) based on NADPH requirement
LED	Light-emitting diode
LMA	Leaf mass per area (m^2)
NADPH	Reduced form of Nicotinamide adenine dinucleotide phosphate
PAM fluorometer	Pulse-amplitude modulated fluorometer
PAR	Photosynthetic active radiation (µmol m^{-2} s^{-1})
PET	Potential evapotranspiration (mm/h)
PPFD	Photosynthetic photon flux density (400 – 700 nm) (µmol photons m^{-2} s^{-1})
PSI	Photosystem I
PSII	Photosystem II
R_d	Mitochondrial respiration rate in the light (µmol m^{-2} s^{-1})
R_D	Dark respiration (µmol m^{-2} s^{-1})
RuBisCO	Ribulose-1,5-bisphosphate carboxylase/oxygenase
SRC	Short rotation coppice
TARMAG	Biodiversity and Target Management of Endangered and Protected Species in Coppice and Coppice-With-Standards Included in System of NATURA 2000 – project supported by the Ministry of the Environment of the Czech Republic for 2007 - 2011
TFE	Training Forest Enterprise Masaryk Forest Křtiny

TPU	Triose phosphate utilisation
V_{Cmax}	Maximum rate of Rubisco carboxylation (μmol m^{-2} s^{-1})
VPD	Vapour pressure deficit (Pa)

1 INTRODUCTION

Plant growth and all physiological functions are tightly connected to the climate and its changes. Plants are more easily exposed to biological damage, e.g. caused by drought, than any other living organisms (Tkemaladze and Makhashvili 2016). From all the resources which plants need to grow and function is water the most abundant and often most limiting and stressful (Taiz and Zeiger 2010). This stressful moments are the key element in diversifying and seeking fundamental distinctions between various forest forms.

In history, coppice was one of the most used and also most important ways of forest management used across whole Europe and even worldwide (Harmer 2004; Kadavý and Kneifl 2007; Matula et al. 2012; Šplíchalová et al. 2012; Adamec et al. 2014; Svátek and Matula 2015; Holišová et al. 2016; Pietras et al. 2016). During last 150 years was this kind of management abandoned and coppices were converted into the high forests (Matula et al. 2012). Nowadays, after setting up the strategy and action plan by European Union White Paper (1997), has coppice management arisen again (Kuiper et al. 1998). Mostly for the reduction of the fossil fuels consumption shifted to renewably resources using coppice biomass production (Holišová et al. 2016), but in a lesser content also because of nature conservation (Matula et al. 2012). Coppice and coppice with standards are also very good way of management for small-scale forest owners (Dreslerová and Svátek 2009).

However, there can be found advantages and disadvantages of both forms of forest management, also from the ecological point of view. This thesis aims to find if sprouting coppice can have better results of physiological functions like photosynthesis, conductance, quantum yield, photosynthesis and water status compared to mature high forest. Moderate drought conditions of vegetation season of 2016 were helpful to distinct differences under the water stress.

When compared coppice with high forest, in first stages of growth has the coppice great benefit of using yet functionally build root system from the maternal tree. Plants of vegetative origin have to invest energy into both, above-ground part and also into root system. Thus, young sprouts of the coppice can utilize this benefit and have the higher photosynthesis rate and assimilation of substances important for plant growth.

2 THESIS OBJECTIVE

The aim of this thesis is to compare differences in plant water status and photosynthesis among various forest forms, especially between coppice and high forest at research plot Soběšice, during the vegetation season of 2016. This comparison is based on several physiological parameters (i.e. photosynthesis, water potential, chlorophyll fluorescence) on the set of sessile oaks growing in the high forest (generative origin), coppice with standards and coppice forest (vegetative origin) capturing their physiological seasonal variability. Results are later discussed with focus on comparing advantages and disadvantages of coppice and high forest management under water stress.

3 LITERATURE OVERVIEW

There are a lot of papers focused on relationship between climate and plant physiological functions as for instance a photosynthesis, conductance or transpiration (Collatz et al. 1991; Whitehead 1998; Medrano et al. 2002; Xu and Baldocchi 2003; Flexas et al. 2014; Gururani et al. 2015; Tkemaladze and Makhashvili 2016). On the other hand not many sources that cover physiological differences between coppice and high forest, which is the main focus of this thesis, can be found.

In the Czech Republic were established several experimental research plots allowing to study conditions of different forest managements, e.g. two TARMAG (Biodiversity and Target Management of Endangered and Protected Species in Coppice and Coppice-With-Standards Included in System of NATURA 2000 – project supported by the Ministry of the Environment of the Czech Republic for 2007 - 2011) sites conducted at the Training Forest Enterprise Masaryk Forest Křtiny belonging to Mendel University in Brno. They were established to simulate the influence of coppice and coppice with standards management and to provide “field laboratory” to concentrate a wide spectrum of analyses into a single space, time and scheme (Kadavý et al. 2011).

3.1 History of coppice management

Foresters use word “coppice” to cover many things including a type of woodland consisting of periodically cut trees, the multi-stemmed trees, the process of felling trees and the production of new shoots by recently cut stools (Harmer 2004).

The management of woodlands as a coppice has very long history with the evidence also from the prehistoric times (Evans 1992; Harmer 2004; Kadavý et al. 2011; Matula et al. 2012; Svátek and Matula 2015; Holišová et al. 2016; Pietras et al. 2016). During the 17th and 18th centuries coppice not only continued to supply building and fencing materials and firewood but was also increasingly in demand for charcoal for the iron and glass industries (Evans 1992). Until 150 years ago it was the most widespread silviculture practice, later converted into the high forest (Evans 1992; Svátek and Matula 2015; Pietras et al. 2016). This decline accelerated after the First World War with coming of other more convenient energy sources (Evans 1992) and socio-economic changes (Svátek and Matula 2015). However, during last two or three decades there has been renewed interest in restoring coppices, primarily for a biofuel, pulp wood and nature conservation (Harmer 2004; Matula et al. 2012; Svátek and Matula 2015; Pietras et al. 2016).

Nowadays, the implementation of wood short rotation coppice (SRC) cultivations could represent an energy and environmental sustainable solution to provide biomass to the power plants, which can reduce energy dependency. However, the biomass yield depends on the climatic conditions, soil, cultivation and management (Pereira and Costa 2017). Compared to fossil fuels it is carbon neutral and produces 80% less sulphur emissions during combustion (Proe et al. 2002).

From the environmental point of view, growing SRCs is accompanied by positive impacts on soil protection, site nutrient capture and retention, improvement of water and air quality, carbon sequestration and biodiversity (Isebrands and Karnosky 2001). Bird and insect populations are enhanced due to complex coppice structure and diversity (Proe et al. 2002).

3.2 Coppice and high forest differences

One of the most important distinctions among silvicultural systems is in various managements between coppice and high forest. In coppice are small-sized repeated crops of vegetative origin regenerated at short intervals by cutting from the stumps, whereas in high forest grow single-stemmed trees from seed or transplants to their full height (Mitchell 1992; Harmer 2004). The coppice with standards, the transition between previous two management systems, is characterized by the cultivation of standards of generative origin over coppice layer for two, three or more rotation periods while the lower storey is usually intended for firewood production and upper storey produces timber, frequently of excellent quality. The number of standards should be as high as to allow the lower coppice storey to thrive (area shaded by standards should not drop below 10% nor exceed 30% of total area) (Kadavý et al. 2011).

The basic method of coppicing is very simple and relies only on ability of trees to regrow from the stumps (Harmer 2004; Matula et al. 2012; Šplíchalová et al. 2012; Svátek and Matula 2015). The easiest way of transition from high forest into coppice is to clear-fell woodland comprising single-stemmed trees. Repeated felling produces the multi-stemmed stools, which are typical for coppice (Harmer 2004).

Sprouting shoots of coppice can originate from roots, underground stems, and the base of the tree and from dormant buds (Bond and van Wilgen 1996). Kadavý et al. (2011) mentioned, that sprouting of coppice forest is maintenance-free, there is a strong regeneration and growth from well coppiced stumps, though (Mummery et al. 1997). From the economic point of view, the coppice has low-managing costs, thus it is very good possibility for small and medium scale forest owners (Dreslerová and Svátek 2009; Holišová et al. 2016). Also the vegetative regeneration is easier than regeneration by seedlings. However, lower quality of timber production, reduced genetic diversity of sprouts leading to decreased plasticity of response to environmental changes (Lloret et al. 2004). Frequent removal of standing biomass in coppice may lead to depletion of soil nutrients (Kadavý et al. 2011). On the other hand, coppice has proved to be more advantageous for the slope stabilization (Pietras et al. 2016).

The presence of existing stump root system in sprouting coppices is one of the most important difference between forest managements. It positively influence starting growth rates of new sprouts because they can utilize existing root system, while the seedlings invest energy into building (Sakai and Sakai 1998; Von Fircks and Sennerby-Forsse 1998; Lloret et al. 2004; Dickmann 2006; Holišová et al. 2016; Pietras et al. 2016). Because of this sprouts are able to develop faster the above-ground part, whereas the seedlings have to invest their energy obtained from photosynthesis into the underground growth. The initial reduced ability of seedlings to uptake resources from the soil makes them more susceptible to water and nutrient insufficiency (Pietras et al. 2016). Nevertheless, Holišová et al. (2016) found that this does not entail a higher photosynthetic ability of sprouts. Indeed, seedlings allocating assimilated carbon to below-ground biomass can have the same or even a higher photosynthetic rate than sprouts, though their above-ground growth can be smaller (Drake et al. 2009). Especially under drought conditions sprouts are able to benefit from the developed root system which allows a higher water uptake compared with seedlings (Lloret et al. 2004).

Pietras et al. (2015) supported the hypothesis that sprouts have access to a larger water pools using the old stump root system especially during the drought. Similarly she also claimed that sprouts seem to be less susceptible to unfavourable climatic conditions than seedling of similar age which is making coppice as more advantageous group on sites with frequent drought periods. In order to provide more reliable results about water use of any kind of vegetation must be used combination of several methods (microclimatological, physiological and hydrological; Fisher et al. 2013). Furthermore, Pietras et al. (2015) found that the sprouts of the same age as seedlings had higher biomass amount and size.

Stojanović et al. (2015) examined sessile oak responses under different light conditions. Their study proved the advantages of young coppice over standards during severe drought. Results showed higher quantum yield in standards under mature canopy, while maximum of coppice was shifted toward the edge light conditions.

Another variability between high forest and coppice can be found in species composition, because not every broadleaved species is able to sprout. Woody plants are divided into two categories – sprouters and non-sprouters (Wildy and Pate 2002; Matula et al. 2012). Mostly seen coppice species in European conditions are Sessile oak (*Quercus petraea* (Mattuschka) Liebl.), European hornbeam (*Carpinus betulus* L.), small-leaved lime (*Tilia cordata* Mill.), Silver birch (*Betula pendula* L.), European aspen (*Populus tremula* L.) (Šplíchalová et al. 2012; Adamec et al. 2014; Svátek and Matula 2015), Holm oak (*Quercus ilex* L.), chestnut (*Castanea sativa* Mill.) and as the SRC also *Populus* and *Salix* species and clones (Harmer 2004; Orság et al. 2012; Fisher et al. 2013), in South Europe used to sprouts also *Eucalyptus* species. Conifers are usually bad sproutes, while very good in high forests.

In even-aged plantations is a canopy closure more uniform, but there is no reason to expect differences between coppice and high forest, unless the details of canopy closure become important (Buckley 1992). For a given density of stools and energy of growth, coppice will reach the canopy closure more quickly than a high forest stand (Mitchell 1992).

Microclimate of coppice and high forest may differ a lot. There are differences in measuring air temperature in incomplete and closed canopy. In incomplete canopy can be average 24 hour temperature about 2 – 3 °C higher during the late spring and early summer than under the closed canopy. The amplitude between night and day temperatures was greater for sites with lower or incomplete canopies. Same conditions would be expected in high forest stands at the same density stages (Mitchell 1992). Furthermore, sprouts on a single stump might create a more favourable microclimate by self-shading (Holišová et al. 2016)

Comparing rotations, the difference between high forest and coppice is simple – rotation period in high forest is 50 – 200 years but young stage of coppice recurs every 10 – 20 years (Mitchell 1992), clonal stands of *Populus* spp. and *Salix* spp. are rotated usually each 2 – 4 years. Mixed broadleaved coppice woodlands managed to produce fuel and small-diameter wood, may be cut on 20-years rotations with some stools capable of surviving for centuries (Harmer 2004).

4 MATERIAL AND METHODS

The current investigation involved measuring of photosynthesis, stomatal conductance, quantum yield, chlorophyll fluorescence and plant water status using infrared gas analyser with fluorescence head and pressure chamber to examine the variance in these variables between different forest forms – coppice, coppice with standards and high forest. The site was selected from the part of Training Forest Enterprise of Mendel University in Brno and has been frequently used to interpret coppice evolution in typical European conditions. In total 24 oak trees were measured for physiology mentioned earlier during the whole vegetation season of 2016.

4.1 Research plot Soběšice

This study was conducted with the experimental site within the Vranov Forest District, Training Forest Enterprise Masaryk Forest Křtiny (special purpose facility) belonging to Mendel University in Brno, located on southeast of the Czech Republic, approximately 2 km SW of the Soběšice municipality (GPS localization: 49°14'42.629" N, 16°35'59.736" E) (Kadavý et al. 2011; Holišová et al. 2016; Pietras et al. 2016). The localization is shown in Figure 1 below. Altitude of research plot is 300 m a. s. l. (Pietras et al. 2016).

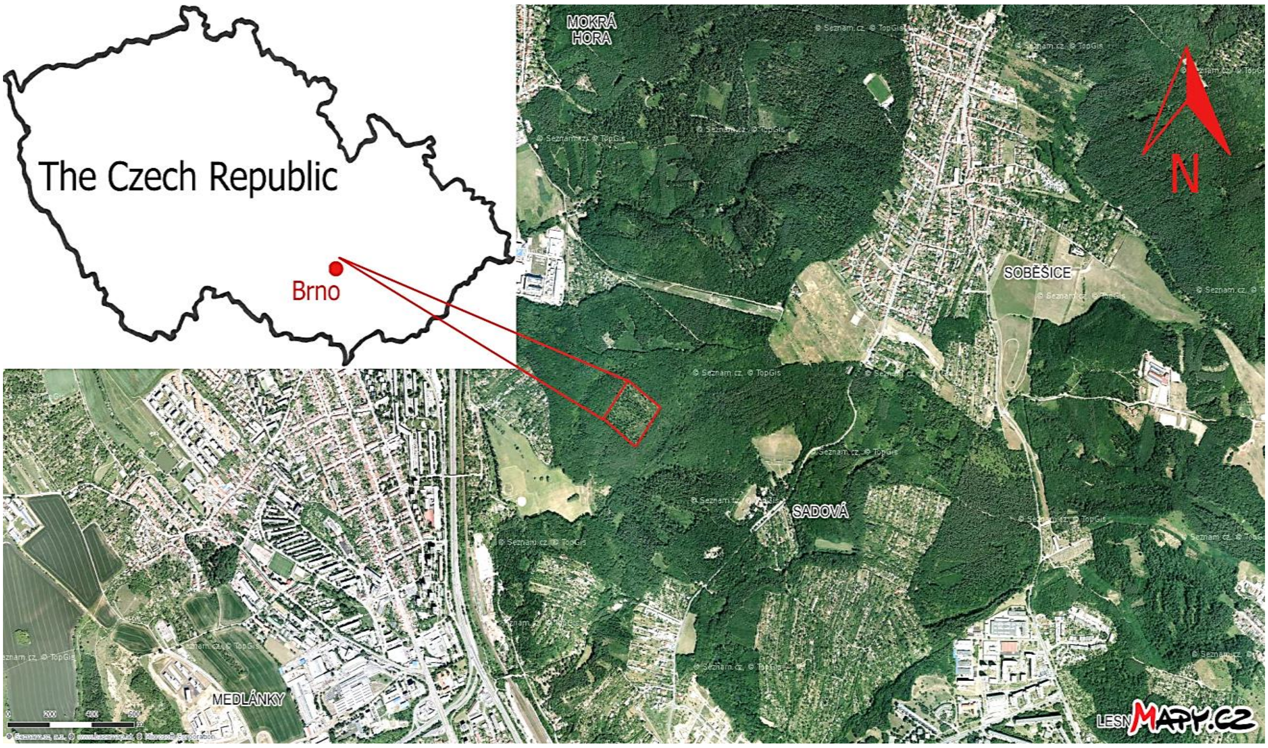

Figure 1: Localization of experimental plot Soběšice (source: www.mapy.cz, adjusted by author).

4.1.1 Climatic and natural specifications

The annual mean temperature at the site is 7.5 °C (Holišová et al. 2016; Pietras et al. 2016). According to Brno weather station is the average air temperature in the warmest month 18.4 °C (July) whereas the coldest monthly average is -2.1 °C (in January) (Matula et al. 2012). The average annual precipitation is varying between 550 and 650 mm (Holišová et al. 2016; Pietras et al. 2016).

According to MapServer TFE Krtiny (http://mapserver-slp.mendelu.cz) the bedrock is granodiorite with small part composed of sediments and the soils are forest cambisols.

Originally the main forest type was rich oak-hornbeam forest with meadow-grass and soft leaved sedge on a plateau and rounded ridges (1B1) and the forest type covering a smaller part is dry oak-hornbeam forest with meadow-grass on slopes (1C2) in exposed stands at lower altitudes (Czech Forest Typology System, Kadavý et al. 2011).

4.1.2 Original and present management of research plot Soběšice

For at least 200 years forest was actively coppiced. Later, after 1902 the coppice was transformed into a high forest (Kadavý et al. 2011). At the turn of 2008 and 2009 there was established 4 ha (200 x 200 m) experimental plot by harvesting approximately 70 years old forest formed by 95 % of sessile oak *Q. petraea* (Pietras et al. 2016) to make a short-rotation coppice system (Matula et al. 2012). The plot is divided into sixteen squares with the same dimensions (50 x 50 m, area 2500m^2) but with different treatments (Kadavý et al. 2011; Holišová et al. 2016). One quarter of squares was clear-felled (without standards left on the plot), the second quarter was harvested with very high intensity (20 trees per plot left), third quarter was harvested with high intensity (35 trees per plot left), and the last quarter was harvested with medium-high intensity (50 trees per plot left – the biggest number of standards per area) (Kadavý et al. 2011; Matula et al. 2012). Research plot belongs to TARMAG (Biodiversity and Target Management of Endangered and Protected Species in Coppice and Coppice-With-Standards Included in System of NATURA 2000 – project supported by the Ministry of the Environment of the Czech Republic for 2007 – 2011) experimental research plots.

Nowadays, the stand is characterized by the presence of seedlings naturally regenerated from seeds of left standards and sprouts grown as a multi-stem coppice from the stumps, with an average of 12 sprouts per stump (Holišová et al. 2016).

4.1.3 Study trees

All measured trees are *Q. petraea*. Distribution of the trees is described later in chapter 4.1.4 connected with map also in this chapter. Dimensions with averages and standard deviations of the trees connected with their individual numbers and localization are shown in table (Tab. 1) below. Heights were measured individually by hypsometer and tape. Diameters of mature trees in high forest were measured at breast height (DBH; in 1.3 m), while diameters of coppice sprouts and young seedlings were measured according to Matula et al. (2012) between 5 and 10 cm above ground, in case of coppice on five thickest sprouts, but in all cases precisely by calliper.

Table 1: Examined trees and their diameters (at breast height (DBH, in 1.3 m) or 5 – 10 cm above ground in case of seedlings and coppice), heights, and averages and standard deviations of both variables.

Square number	Individual number	Type of individual (forest form)	DBH [mm] / diameter in 5 - of10 cm above ground	Height [m]	Average DBH [mm]	Standard deviation of DBH	Average height [m]	Standard deviation of height	Average DBH [mm]	Standard deviation of DBH	Average height [m]	Standard deviation of height
1	67	A_coppice	89 71 46 51 34	3.55	64.33	16.52	3.60	0.13	61.00	16.90	3.53	0.38
1	603	A_coppice	96 70 61 53 59	3.50								
1	609	A_coppice	84 65 71 56 59	3.75								
9	2036	A_coppice	91 97 51 51 56	3.80	57.67	17.17	3.45	0.56				
9	2048	A_coppice	62 66 61 49 34	3.75								
9	2052	A_coppice	54 54 54 51 34	2.80								
2	231	B_coppice	40 49 40 34 30	2.80	39.53	10.14	3.27	0.64	38.80	9.88	3.03	0.55
2	237	B_coppice	41 65 39 28 31	3.00								
2	759	B_coppice	52 46 37 29 32	4.00								
10	2093	B_coppice	45 36 38 29 28	2.60	38.07	9.92	2.80	0.44				
10	2095	B_coppice	52 59 40 38 30	3.30								
10	2101	B_coppice	50 33 36 35 22	2.50								
9	S1	A_seedling	13	0.83	11.67	1.53	0.74	0.14	14.00	3.74	14.00	0.10
9	S2	A_seedling	12	0.81								
9	S3	A_seedling	10	0.58								
1	S4	A_seedling	21	0.75	16.33	4.04	0.69	0.07				
1	S5	A_seedling	14	0.70								
1	S6	A_seedling	14	0.62								
-	HF1	C_highforest	295	17.00	279.33	13.58	16.53	0.64	272.83	17.97	17.02	0.87
-	HF2	C_highforest	271	16.80								
-	HF3	C_highforest	272	15.80								
-	HF4	C_highforest	292	18.50	266.33	22.28	17.50	0.89				
-	HF5	C_highforest	255	16.80								
-	HF6	C_highforest	252	17.20								

4.1.4 The experimental design

The study presented in this thesis was conducted at four squares of research plot Soběšice, two squares with clear-felled management (squares 1 and 9) and two squares which are harvested with medium-high intensity (squares 2 and 10). Within these squares coppiced trees (12 individuals) were measured, in clear-felled squares also seedlings (6 individuals). On the north boundary between experimental plot and high forest 6 measured individuals were located in the high forest. Six plants from each group (seedlings, coppice, and high forest) were selected within the plot. All of these measured individuals with their localization are shown in appended figure (Supplementary figure 1). Measured sprouting coppice individuals located in squares 1 and 9 are marked as “A_coppice”, individuals growing within the squares 2 and 10 are marked as “B_coppice”, seedlings growing in squares 1 and 9 are marked as “A_seedling” and trees from high forest are marked as “C_highforest”.

Physiological measurements were conducted after the vegetation season of 2016 started, however the oak leaves needed to be fully developed. First measurement was in June (7th) and then it continued in nearly monthly intervals (7th July, 4th August, 30th August and 28th September). During each of the dates photosynthesis, chlorophyll fluorescence and plant water potential were measured at noon. In the morning dark fluorescence and predawn leaf water potential was measured. On the 23rd August were leaves picked for an analysis of leaf mass per area. Light curves and CO_2 response curves (also known as A-C_i curves) were carried out before leaf yellowing between 22nd and 31st August. Each day of measurement was a sunny day without precipitation. The plants were measured in random order.

4.1.4.1 Soil and weather measurements

During the whole vegetation season, from March to September, was the volumetric water content of soil measured every two weeks using FieldScout TDR 300 moisture meter (Spectrum Technologies, Inc., IL, USA). On the plots 6 and 10 were also continuously monitored soil water content and soil water potential (Gypsum blocks GB2 (Delmhorst, Inc, USA) attached to data logger SP3 (EMS Brno, Czech Republic) and CS650 (Campbell, Inc., Logan, USA) attached to MicroLog SDI-CS data logger (EMS Brno, Czech Republic), respectively) together with climatic variables: global radiation (EMS 11, EMS Brno, Czech Republic), air temperature (EMS 33, EMS

Brno, Czech Republic), relative air humidity (EMS 33, EMS Brno, Czech Republic), wind speed (WindSonic, GILL, Hampshire, UK) and precipitation (Rain-O-Matic Professional, Pronamic, Ringkobing, Denmark) attached to datalogger EdgeBox V8 (EMS Brno, EMS Brno, Czech Republic). Potential evapotranspiration (PET) was calculated according to FAO equations (Allen et al. 1998). Vapour pressure deficit (VPD) was calculated from measured air temperature and the relative humidity.

4.1.4.2 Water potential

Plant water potential (Ψ_w) was measured two times per observation day. Once during the peak (noon) of the day between 11 a.m. and 15:30 p.m. and once as a predawn water potential (the time of measurement was dependent on time of dawn), in both cases on the sun-exposed leaf. Leaves were cut from the branches and water potential was measured by a pressure chamber, type PMS 1000 (PMS Instrument Company, Albany, OR, USA). Pressure in chamber was raising with the speed 0.02 MPa s^{-1} until the water drop appeared on the cut area of the petiole.

4.1.4.3 Photosynthesis, stomatal conductance and quantum yield

On every plant a sun-exposed (and fully developed) leaf was measured between 11 a.m. and 15:30 p.m. Portable infrared gas analyser LI-6400 (LI-COR Inc., Lincoln, Nebraska, USA) with LI-6400-40 Leaf Chamber Fluorometer (LI-COR Inc., Lincoln, Nebraska, USA) were used.

Assimilation parameters – the light-saturated CO_2 assimilation rate (A_{max}), the transpiration rate (E), the stomatal conductance (g_s) were measured together with quantum yield (Φ_{PSII}) and other parameters (i.e. leaf and air temperature, relative humidity). Every time the leaves were exposed to same conditions in the chamber set by LI-6400 and LI-6400-40: the air flow rate 300 $\mu mol.s^{-1}$, the ambient CO_2 concentration 400 $\mu mol\ CO_2\ mol^{-1}$ and the saturated photosynthetic photon flux density (PPFD) 1500 μmol photons $m^{-2}\ s^{-1}$ (with 10 % of blue light). Air humidity and temperature in leaf chamber followed the actual environmental conditions. Leaf area closed into the chamber was 2 cm^2.

4.1.4.4 Fluorescence

Fluorescence was measured by the LI-6400-40 Leaf Chamber Fluorometer sensor head (LI-COR Inc., Lincoln, Nebraska, USA) attached to the LI-6400XT (LI-COR Inc., Lincoln, Nebraska, USA) gas analyser. The LI-6400-40 is a pulse-amplitude modulated (PAM) fluorometer which can be used to take measurements on both light- and dark-adapted samples. It provides complete control over the actinic and saturation (independently controlled red 630 nm and blue 470 nm LEDs), measuring (red 630 nm LEDs, modulated from 0.25 to 20 kHz) and far-red (740 nm LED for PSI excitation) light. Leaf area closed into the chamber was again 2 cm^2.

Fluorescence was measured during exactly same conditions and same time like day and predawn water potential and on the same leaf as photosynthesis, immediately after. Settings for determining $F_{v'}/F_{m'}$ on the light-adapted leaves were following: intensity 5 (of the 2 red measuring LEDs, from the scale 0 to 10), modulation 20 (kHz), filter 1 (Hz), gain 10, flash type rectangular, flash duration 0.8 (s), flash intensity 8, and flash modulation 20 (kHz) and filter 50 (Hz). Therefore settings for determining F_v/F_m on dark-adapted leaves were: intensity 1 (of the 2 red measuring LEDs, scale 1 to 10), modulation 0.25 (kHz), filter 1 (Hz), gain 10, flash type rectangular, flash duration 0.8 (s), flash intensity 7, flash modulation 20 (kHz) and filter 50 (Hz) and actinic light was off. Leaf area closed into the chamber was 2 cm^2.

4.1.4.5 A-C_i curves

A-C_i curves were measured using LI-6400 and LI-6400-40 and user adjusted auto program. The A-C_i curve started at ambient CO_2 concentration of 400 µmol CO_2 mol^{-1}, decreased stepwise to 100, 50 µmol CO_2 mol^{-1} and then increased to 100, 200, 300, 400, 400, 600, 800, 1600 µmol CO_2 mol^{-1} and finished by 400 µmol CO_2 mol^{-1} again. Air flow rate was whole time fixed on 300 µmol s^{-1} and the relative humidity in the chamber was kept above 50%.

A-C_i curves were used for the estimation of CO_2 compensation point (where the photosynthesis and respiration are in balance), stomatal and carboxylation efficiency (maximum rate of Rubisco carboxylation - V_{Cmax}) (Li-Cor 2012), CO_2 saturated assimilation rate (A_{sat}), maximum photosynthesis rate (A_{max}), stomatal conductance (g_m). maximum rate of electron transport (J_{max}), day respiration (R_d) and triose phosphate utilisation (TPU). A-C_i curves were analysed and interpreted by A-C_i Excel Spreadsheets and equations according to Sharkey et al. (2007). Data for all investigated trees were standardized to 25 °C before comparing the results.

4.1.4.6 Light curves

Light response curves measure photosynthetic plant response(s) to light intensity. These measurements explore day respiration rate (R_D), maximum apparent quantum efficiency, light saturated photosynthesis (A_{sat}), light compensation point (I_{comp}, the light level at which photosynthesis equals to respiration), light saturation point beyond which there is no significant change in photosynthesis rate (I_{max}) and light saturation point for photosynthesis + day respiration equal to 50% of maximum photosynthesis rate.

Light curves were also measured using LI-6400 and LI-6400-40 and users adjusted auto program. The light curve started at PPFD 1500 µmol photons m^{-2} s^{-1} (more than ambient), decreased stepwise to 1000, 500, 200, 100, 50, 20 and finished in PPFD 0 µmol photons m^{-2} s^{-1}. Air flow rate was whole time fixed on 500 µmol.s^{-1} and the humidity in the chamber was kept above 50%. Light curves were analysed and interpreted using light curves Excel Spreadsheets (Lobo et al. 2013), Equation 1 (rectangular hyperbola).

4.1.4.7 Leaf mass per area

On the 23rd August were collected leaves for analysis of LMA. Scanner EPSON Perfection V550 Photo created JPG pictures of leaves with scale, which were later analysed using Fiji distribution of ImageJ (Wayne Rasband, Research Services Branch, National Institute of Mental Health, Bethesda, Maryland, USA, 2012) to get the leaf area. Leaf area was later divided by the weight of dried leaves to calculate leaf mass per area (LMA) for photosynthesis. Scanning and measuring of the leaf area was conducted with the weighting newly dried leaves that gave the results of leaf mass per area and its differences between variants of presented experiment.

4.1.5 Data analysis

Calculations were processed by MS Excel 2013 (Microsoft, Redmond, Washington, USA). Collected data were statistically analysed mostly using R 3.3.1 (R Development Core Team, 2016) through statistical environment RStudio 1.0.136 (RStudio Inc., Delaware Corporation, Boston, MA, USA, 2016), some easier parts were performed by STATISTICA 12 (StatSoft, Czech Republic). Firstly, data were tested on normality and homogeneity of variances. Evaluation of the differences among different groups (seedlings, trees, and coppice) and among different dates of measurements was performed by two-way analysis of variance (ANOVA) and Tukey test. To differentiate individual dates and variants for each measured physiologic parameters were used simultaneous tests for general linear hypotheses and multiple comparisons of means using Tukey contrasts. For all analyses was used alpha = 0.05. The ggplot2 package for R (Wickham 2009), STATISTICA 12 (StatSoft, Czech Republic) and SigmaPlot® 12.5 (Systat Software Inc., Chicago, IL, USA, 2016) were used to visualise the results.

5 RESULTS

5.1 Weather and soil measurements

5.1.1 Weather

The precipitation amount during the year 2016 was the 89.9% of the long-term normal (1961 – 1990) according to Czech Hydrometeorological Institute (CHMI) (long-term normal precipitation was 543 mm and precipitation in 2016 was 488.4 mm).

During the vegetation season of 2016 the spring was relatively dry (March - May precipitation of 98.2 mm; 74.4% of long-term normal precipitation of 132 mm), but summer was wet (June - August precipitation of 200.2 mm, 100% of long-term normal precipitation of 200 mm) (Fig. 2A). The wettest month was July with 135.2 mm of precipitation (211.3% of long-term normal precipitation for July). The driest month was September with the amount of precipitation of 7.8 mm (19% of long-term normal precipitation for September).

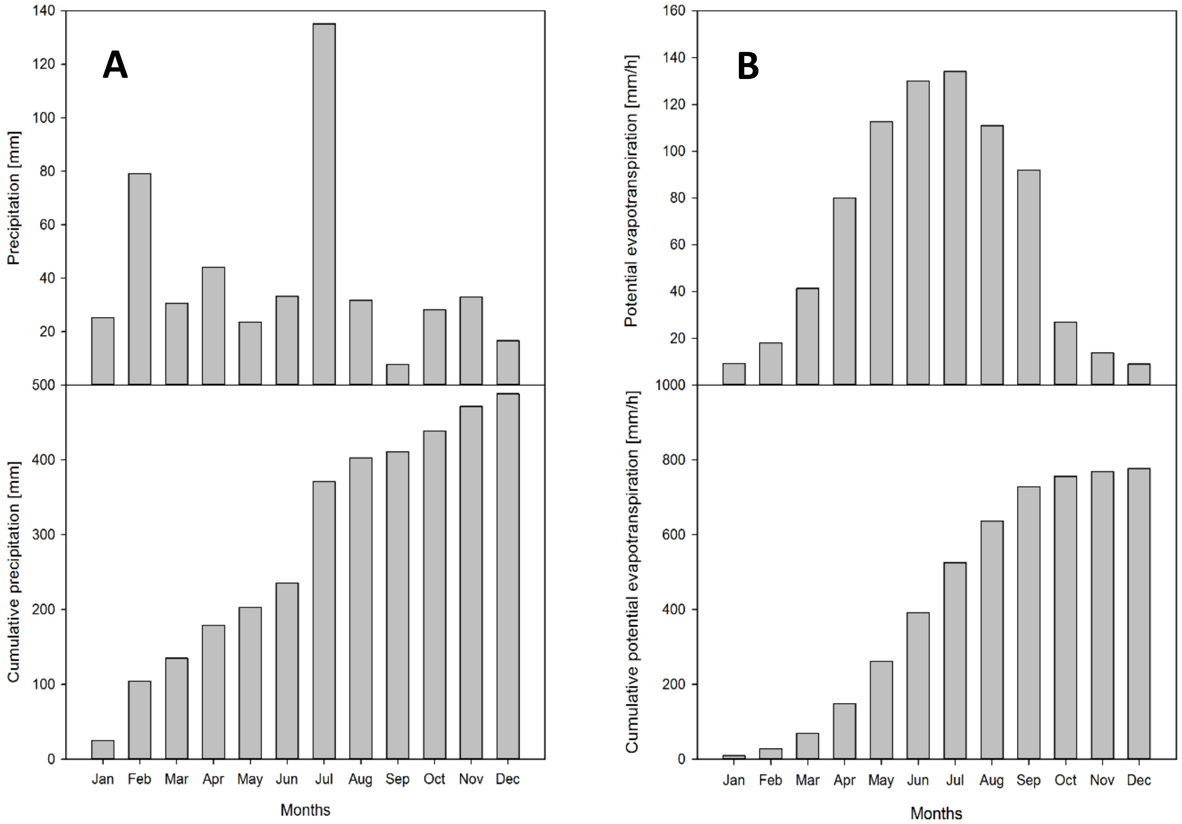

Figure 2:(A) Precipitation during vegetation season of 2016. (B) Potential evapotranspiration through whole vegetation season of 2016.

According to CHMI the air temperature deviation from long-term normal (for years 1961 – 1990) during the whole year 2016 in South Moravian Region was

0.9 °C. Long-term air temperature was 8.3 °C and average temperature of 2016 was 9.2 °C.

The warmest month was July with average month temperature of 19.46 °C (long-term air temperature normal is 18.1 °C for July) and the coldest month was January with average month temperature of -1.94 °C (long-term air temperature normal is -2.6 °C for January). The hottest recorded temperature was on 11th of July with temperature 34.8 °C, while the coldest was on 22nd of January with the temperature -11.8 °C. The highest average day temperature was on 25th of June with the temperature of 27.4° C, whereas the coldest average day temperature was on the 4th of January with the temperature -8.8 °C.

Calculated PET reached 777.4 mm during the year 2016 (Fig. 2B). It was 289 mm more than precipitation and therefore the climatic deficit was 289 mm. The largest difference between PET and precipitation was in June (96.95 mm). The highest monthly average value of PET was in July (134.1 mm), followed by the value in June (130.15 mm). The lowest monthly average value of PET was found in December (8.97 mm, Supplementary figure 2). The highest average global radiation was measured in July (154894.92 W m^{-2}), and with very similar values in June (153732.37 W m^{-2}), while the lowest average global radiation occur in February (32423.4 W m^{-2}; Supplementary figure 2). The highest average value of VPD was recorded in July (492644.68 Pa), followed by value in June (477998.17 Pa), whereas the lowest average value of VDP was in December (34036.3 Pa; Supplementary figure 2). Detailed weather conditions (global radiation, VPD, PET and air temperature) during measuring days are also shown in appended graph (Supplementary figure 3).

5.1.2 Soil

Data obtained from the soil probes measuring soil water potential showed noticeable differences in soil moisture in variants of depths and forest forms (Fig. 3). The highest number of wet events was found in coppice with standards, then in coppice and the lowest number was found in high forest. Variability in soil moisture declined with depth. Type of canopy had an effect on the soil moisture (Fig. 3).

The results of ANOVA and Tukey test analysing the volumetric water content did not show significant differences among individual squares (1, 2, 9, 10; $p = 0.86$) whereas showed the significant differences in results of interaction of date and square number ($p < 0.001$) and different dates of measurements ($p < 0.001$; Fig. 4).

On 15th of July was volumetric water content measured after rainy period which correlates with weather data described in previous chapter. Most important difference is at the beginning of July in square 10 (half of the B_coppice) where the volumetric water content was noticeably higher than on the other squares, whereas in first week of August was this square markedly drier than others.

Soil moisture and volumetric water content should correlate with photosynthesis and conductance, which is depicted in following chapters.

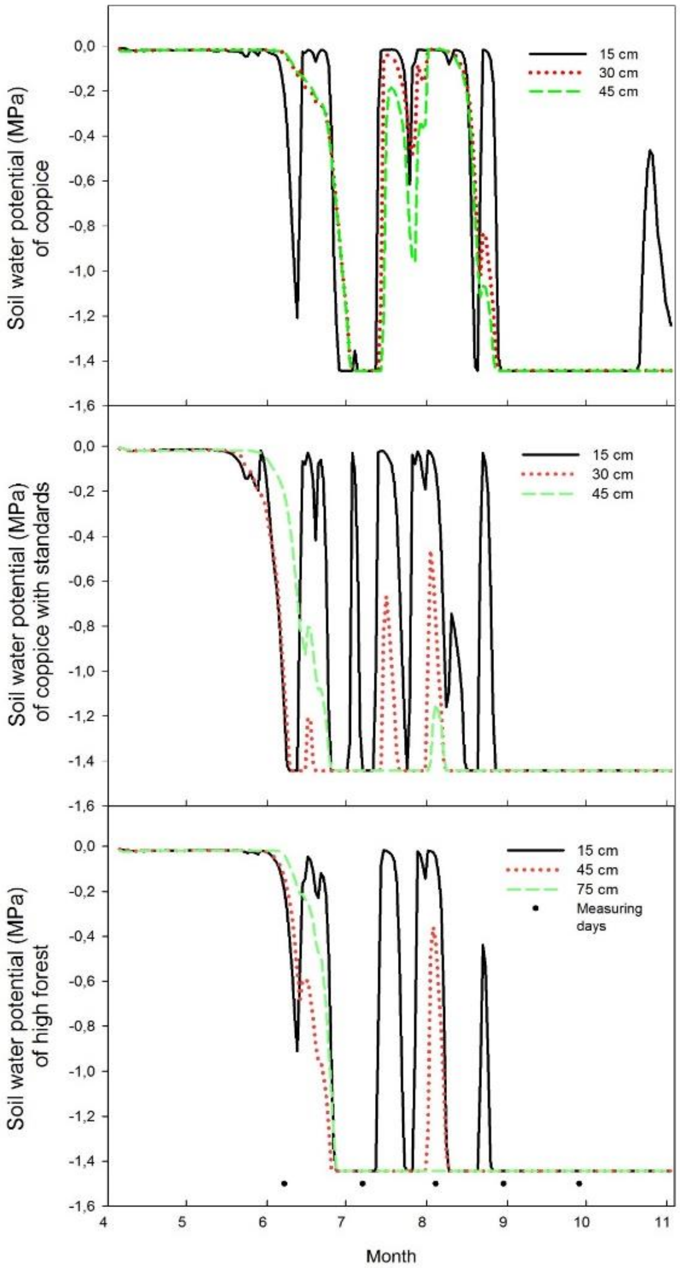

Figure 3: Comparison of soil water potential in different forms of forest (upper part - coppice, middle part - coppice with standards, bottom part - high forest) and different depths of soil probes.

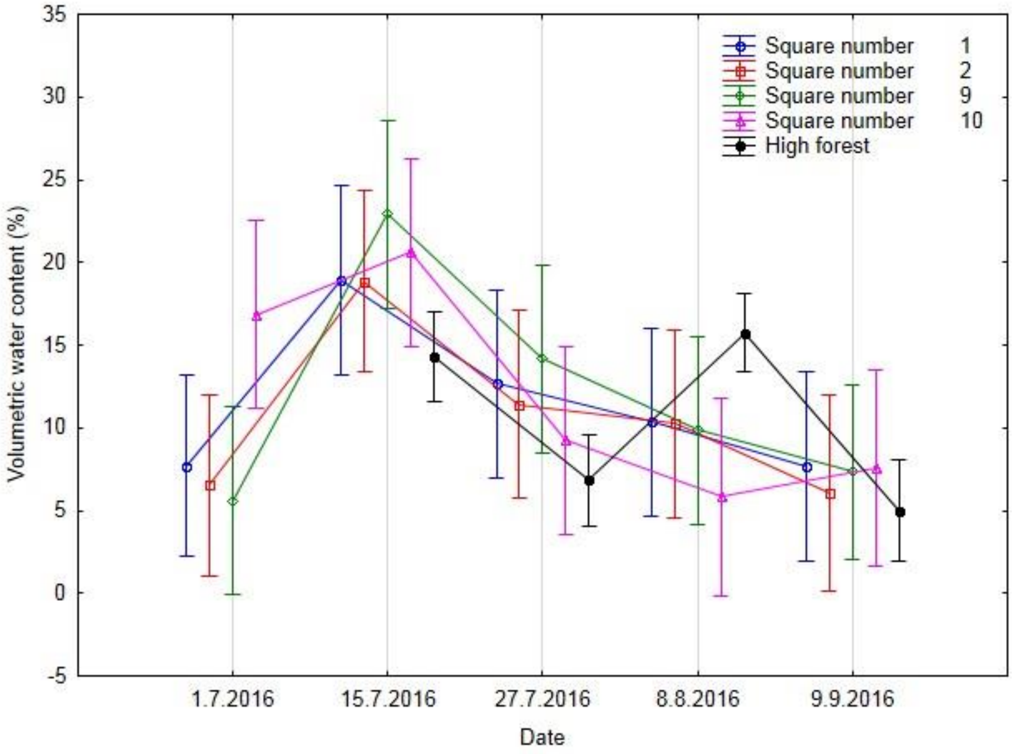

Figure 4: Plot of ANOVA of volumetric water content showing the differences between measurements.

5.2 Water potential

Observation seeking for limitations of water availability by measuring Ψ_w showed, that most stressful period was in September (Fig. 5, Supplementary table 1). The lowest average value of noon water potential was in A_seedling in September with average value of -3.94±0.1 MPa and the highest average value was in A_coppice in June with value of -1.31±0.1 MPa (Supplementary table 1).

Simultaneous tests for general linear hypotheses and multiple comparisons of means using Tukey contrasts showed several significant differences in results of measurements of the noon water potential. The most significant variability was between A_coppice and C_highforest in June ($p < 0.001$) and also between A_coppice and A_seedling in July ($p < 0.001$; Tab. 2, Fig. 5).

*Table 2: Significance of differences between variants in noon water potential. Significant codes for p-value: 0 < '***' < 0.001 < '**' < 0.01 < '*' < 0.05.*

Month	**Interactions**	**p-value**	**Significance**
June	B_coppice - A_coppice	0.0241	*
June	C_highforest - A_coppice	<0.001	***
June	C_highforest - A_seedling	0.0315	*
July	A_seedling - A_coppice	<0.001	***
July	C_highforest - A_coppice	0.027	*
July	B_coppice - A_seedling	0.012	*
End of August	C_highforest - A_seedling	0.00157	**
September	A_seedling - A_coppice	0.00775	**
September	B_coppice - A_seedling	0.00897	**

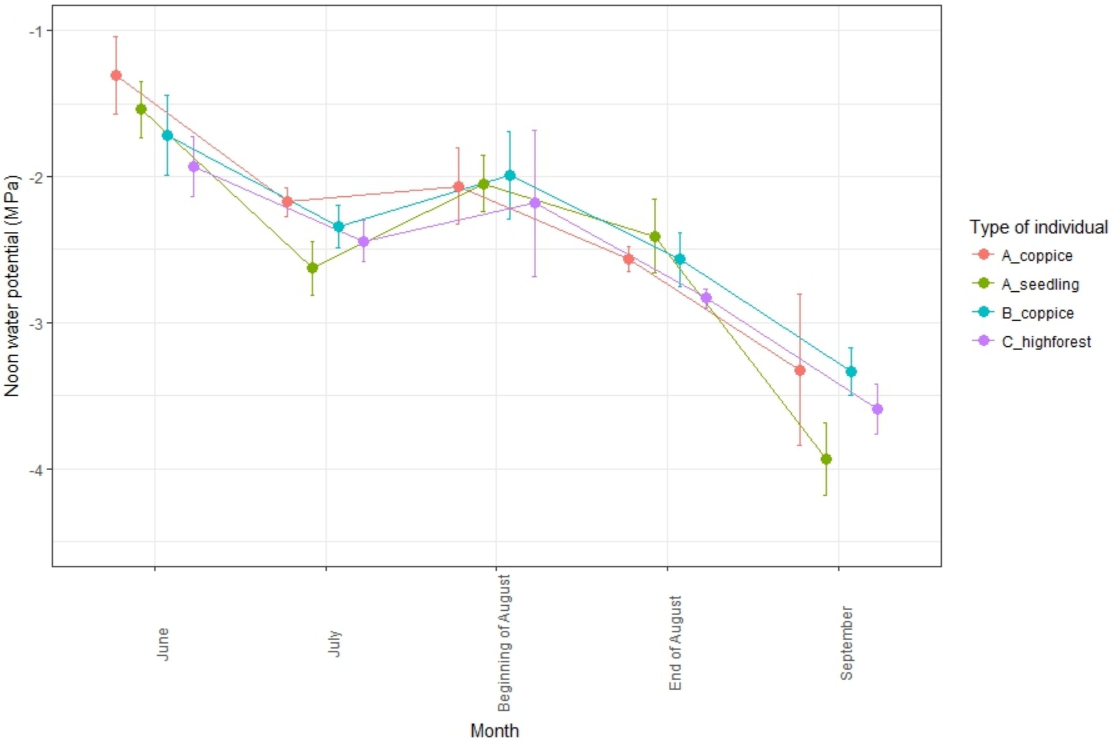

Figure 5: Plotted results of ANOVA showing differences of noon water potential (in MPa) between variants of experiment.

Within the results recorded in predawn water potential was the most limiting value found in C_highforest in September with the value of -3.27±0.07 MPa, while the less limiting value was in A_seedling at the beginning of August with the value -0.23±0.03 MPa (Supplementary table 2).

Largest differences in predawn water potential occurred in July and at the end of August (Table 3, Fig. 6). Most significant were the differences between A_seedling and A_coppice in July ($p < 0.001$), A_coppice and C_highforest in July ($p < 0.001$), A_seedling and B_coppice in July ($p < 0.001$) and B_coppice and C_highforest also in July ($p < 0.001$). During the investigation at the end of August was the significant variability found in case of A_coppice and C_highforest ($p < 0.001$), and A_seedling and C_highforest ($p < 0.001$).

*Table 3: Significance of differences between variants in predawn water potential. Significant codes for p-value: 0 < '***' < 0.001 < '**' < 0.01 < '*' < 0.05.*

Month	Interactions	p-value	Significance
June	A_seedling - A_coppice	0.0114	*
July	A_seedling - A_coppice	<0.001	***
July	C_highforest - A_coppice	<0.001	***
July	B_coppice - A_seedling	<0.001	***
July	C_highforest - B_coppice	<0.001	***
Beginning of August	C_highforest - A_seedling	0.00974	**
End of August	B_coppice - A_coppice	0.0135	*
End of August	C_highforest - A_coppice	<0.001	***
End of August	C_highforest - A_seedling	<0.001	***
End of August	C_highforest - B_coppice	0.0137	*
September	C_highforest - A_coppice	0.0133	*

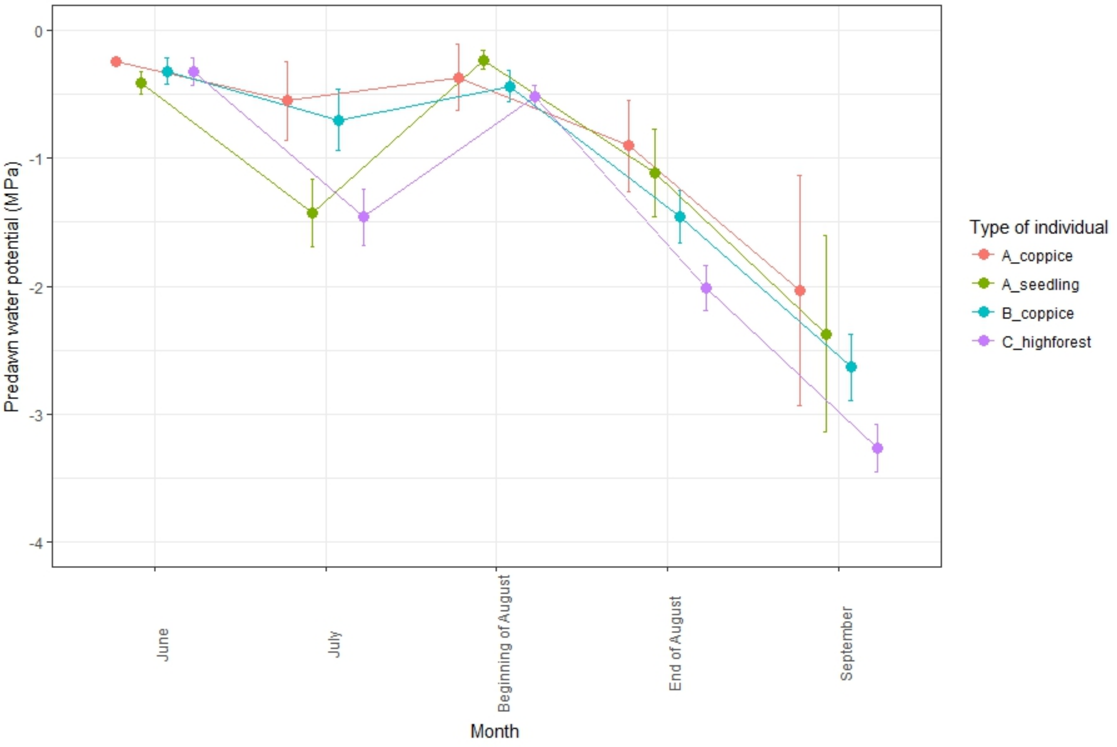

Figure 6: Plotted results of ANOVA showing differences of predawn water potential (in MPa) between variants of experiment.

5.3 Photosynthesis, stomatal conductance and quantum yield

Gas exchange measurements revealed significant differences in results of A, g_s and Φ_{PSII} across all variants and observation days (Supplementary table 3, 4, 5). The highest observed monthly average value of A was in A_coppice at the beginning of August with the value of 15.09±2.0 µmol m^{-2} s^{-1}, whereas the lowest value was in A_seedling in September with the value of 0.86±0.2 µmol m^{-2} s^{-1} (Supplementary table 3). Values of g_s and Φ_{PSII} are closely connected to the A. The highest value of g_s and Φ_{PSII} was again in A_coppice at the beginning of August (g_s = 0.22±0.03 mmol m^{-2} s^{-1}, Φ_{PSII} = 0.27±0.01; Supplementary table 4, 5). However, the lowest values did not followed the same trend like the highest values. The lowest value of g_s was in C_highforest in September with the value of 0.003±0.001 mmol m^{-2} s^{-1} and the lowest value of Φ_{PSII} was again in C_highforest with the value of 0.07±0.006.

The most significant differences in A measurements results were found between A_seedling and A_coppice in June (p = 0.008) and at the end of August among A_coppice and C_highforest (p = 0.004; Tab. 4, Fig. 7).

*Table 4: Significance of differences among variants in photosynthesis. Significant codes for p-value: 0 < '***' < 0.001 < '**' < 0.01 < '*' < 0.05.*

Month	**Interactions**	**p-value**	**Significance**
June	A_seedling - A_coppice	0.00791	**
June	C_highforest - A_seedling	0.02831	*
July	A_seedling - A_coppice	0.0386	*
Beginning of August	C_highforest - A_coppice	0.0152	*
Beginning of August	C_highforest - B_coppice	0.0499	*
End of August	C_highforest - A_coppice	0.00377	**
End of August	C_highforest - A_seedling	0.02241	*

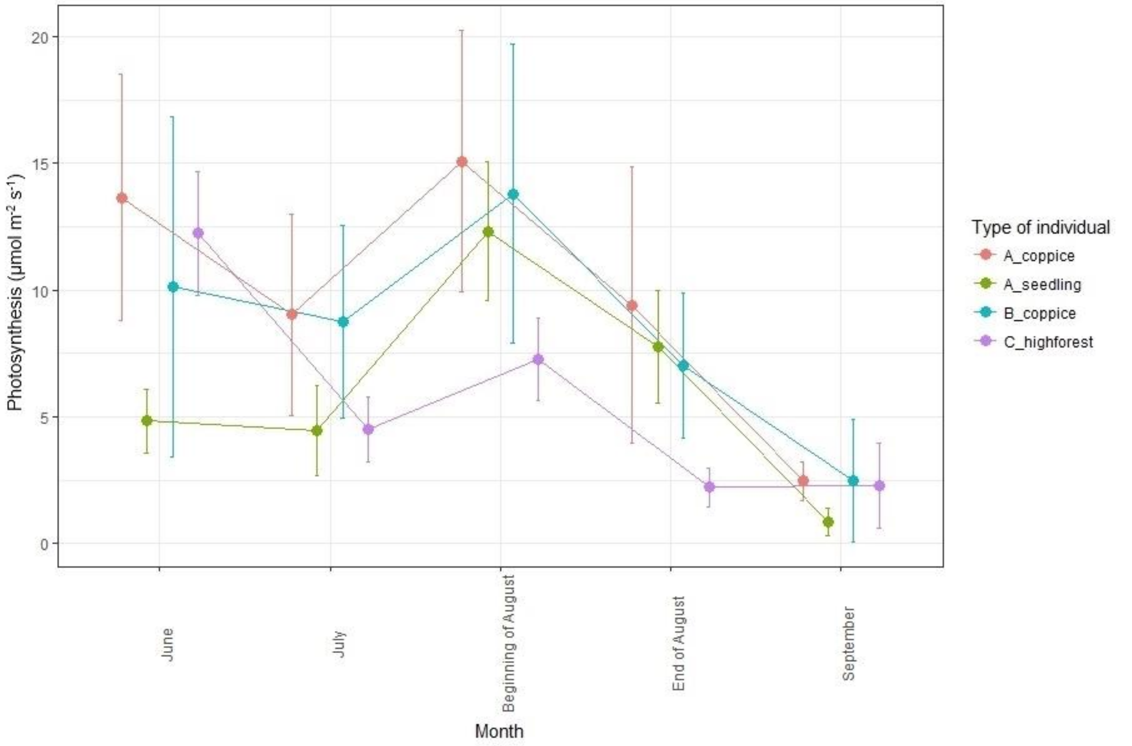

Figure 7: Plotted results of ANOVA showing differences of photosynthesis between variants of experiment.

g_s and A were correlated (Fig. 8). Both of them were lowest in September in all variants, while the highest values were in June and beginning of August (Fig. 7, Fig. 9).

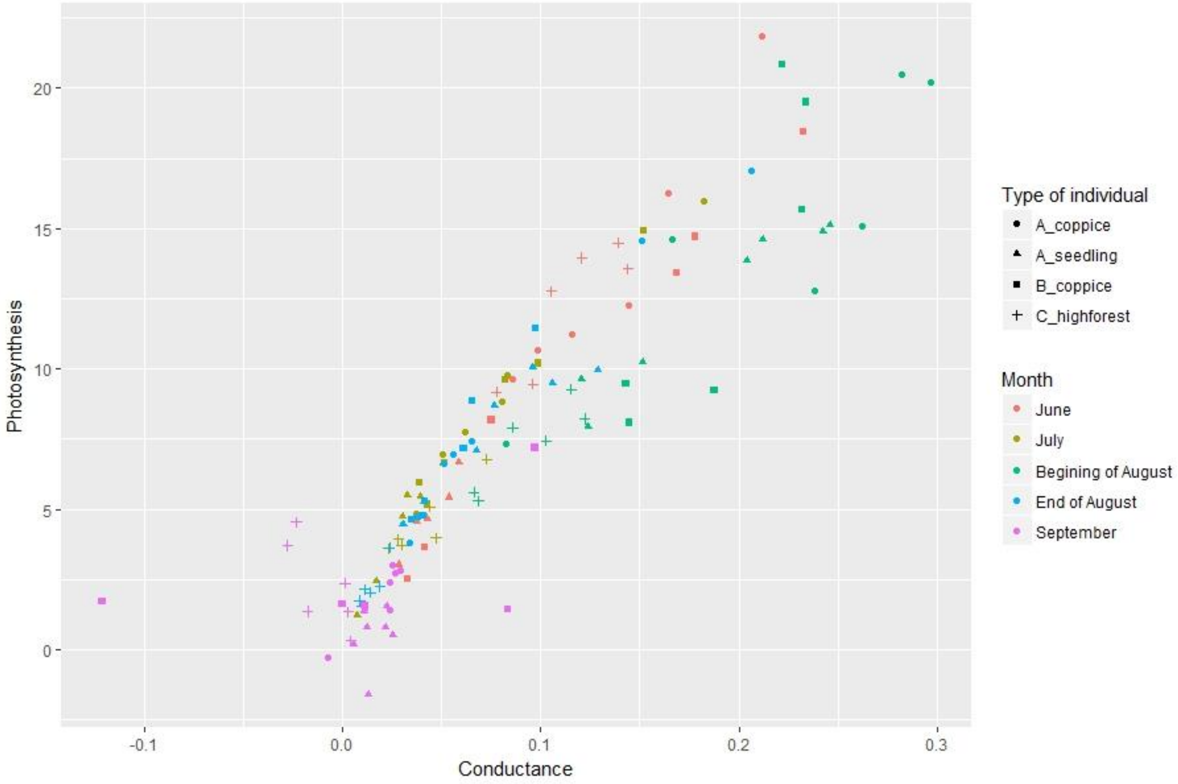

Figure 8: Photosynthesis vs. stomatal conductance at various variants of experiment and dates.

Simultaneous tests for general linear hypotheses and multiple comparisons of means using Tukey contrasts showed several significant differences in g_s. The most significant difference was found between A_coppice and C_highforest (p = 0.003) at beginning of August (Tab. 5, Fig. 9).

*Table 5: Significance of differences between variants in stomatal conductance. Significant codes for p-value: 0 < '***' < 0.001 < '**' < 0.01 < '*' < 0.05.*

Month	**Interactions**	**p-value**	**Significance**
June	A_seedling - A_coppice	0.0191	*
Beginning of August	C_highforest - A_coppice	0.00287	**
Beginning of August	C_highforest - A_seedling	0.02926	*
Beginning of August	C_highforest - B_coppice	0.02149	*
End of August	C_highforest - A_coppice	0.0129	*
End of August	C_highforest - A_seedling	0.0467	*

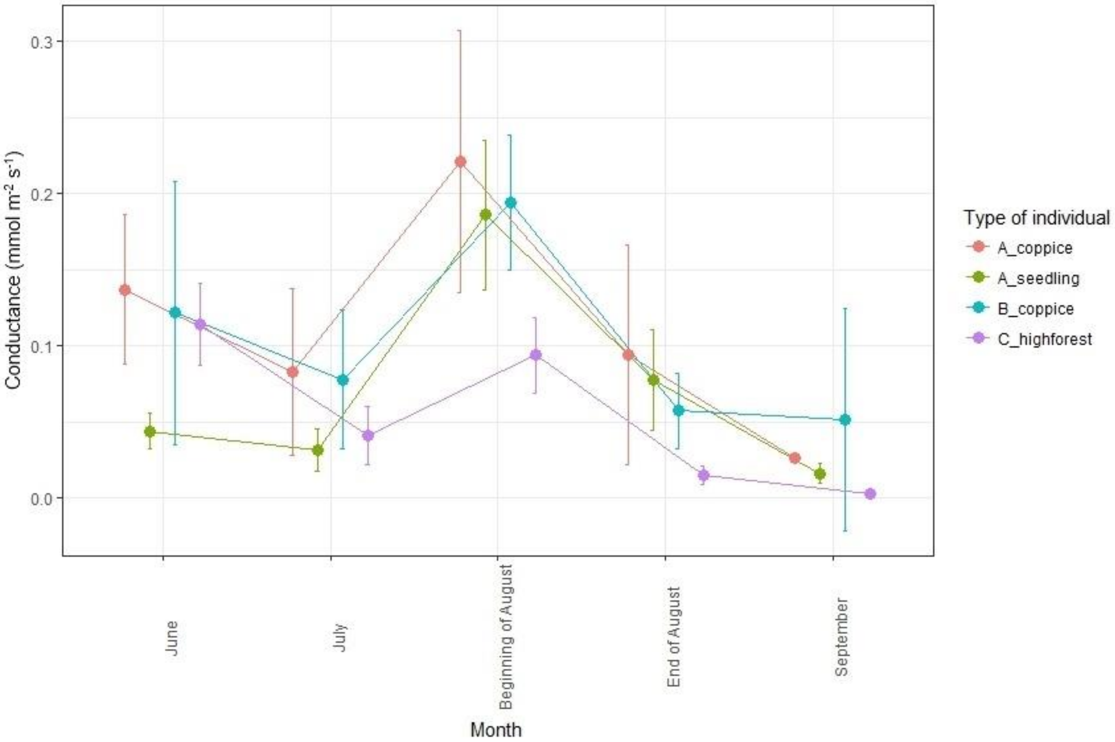

Figure 9: Plotted results of ANOVA showing differences of stomatal conductance between variants of experiment.

The most significant differences of results measured for variable Φ_{PSII} were found between A_coppice and C_high forest (p < 0.001) at beginning of August and again between A_coppice and C_high forest (p < 0.001) at the end of August (Tab. 6, Fig. 10).

*Table 6: Significance of differences between variants in variable quantum yield. Significant codes for p-value: 0 < '***' < 0.001 < '**' < 0.01 < '*' < 0.05.*

Month	Interactions	p-value	Significance
June	A_seedling - A_coppice	0.0267	*
Beginning of August	C_highforest - A_coppice	< 0.001	***
Beginning of August	C_highforest - A_seedling	0.00792	**
Beginning of August	C_highforest - B_coppice	0.01177	*
End of August	A_seedling - A_coppice	0.0373	*
End of August	C_highforest - A_coppice	<0.001	***
End of August	C_highforest - B_coppice	0.0494	*

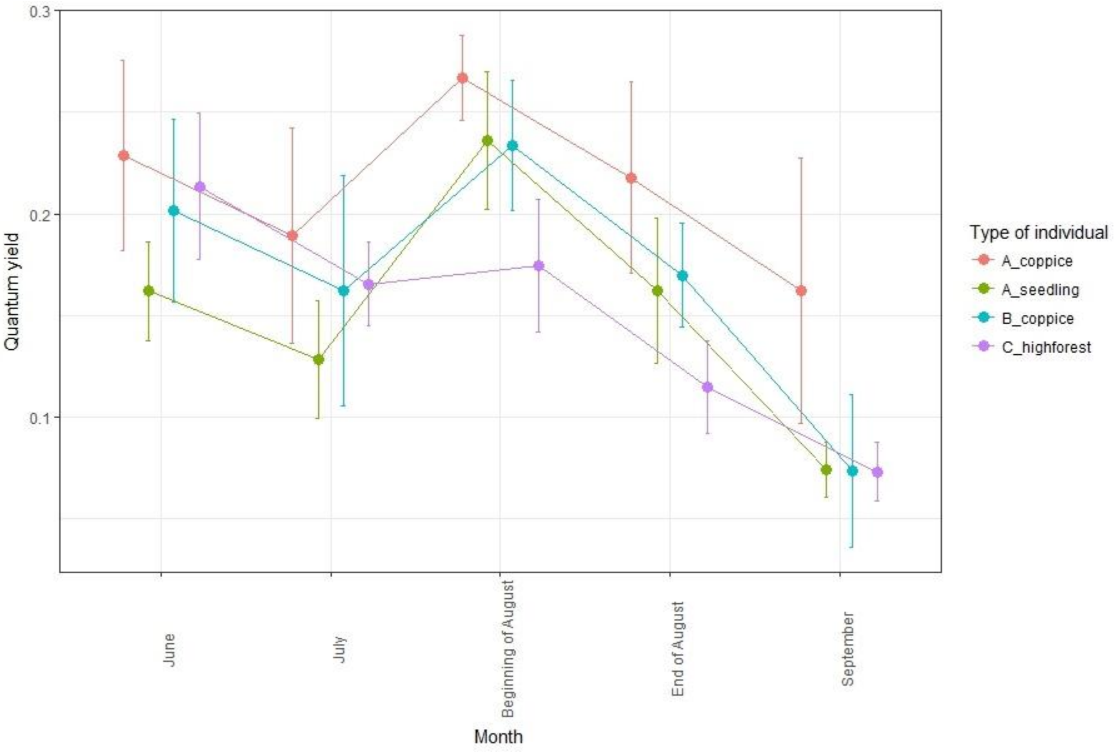

Figure 10: Plotted results of ANOVA showing differences of quantum yield between variants of experiment.

5.4 Chlorophyll fluorescence

During measuring reemitted light energy as a light-chlorophyll fluorescence were found differences between examined variants of this experiment (Supplementary table 6, 7). The highest average value of noon fluorescence was found in A_coppice at the beginning of August with the value of 0.62±0.08 and the lowest average value was found in A_seedling in June with the value of 0.35±0.007 (Supplementary table 6). Predawn fluorescence had the highest average value in C_highforest in June with the value of 0.93±0.02, while the lowest was in A_seedling also in June with the value of 0.82±0.01 (Supplementary table 7).

Testing of variability of results of noon fluorescence showed only two significant interactions, one between A_seedling and C_high forest (p = 0.0386) in June and second between A_seedling and A_coppice (p = 0.0306) at beginning of August (Tab. 7, Fig. 11).

*Table 7: Significance of differences between variants in quantum yield. Significant codes for p-value: 0 < '***' < 0.001 < '**' < 0.01 < '*' < 0.05.*

Month	Interactions	p-value	Significance
June	C_highforest - A_seedling	0.0386	*
Beginning of August	A_seedling - A_coppice	0.0306	*

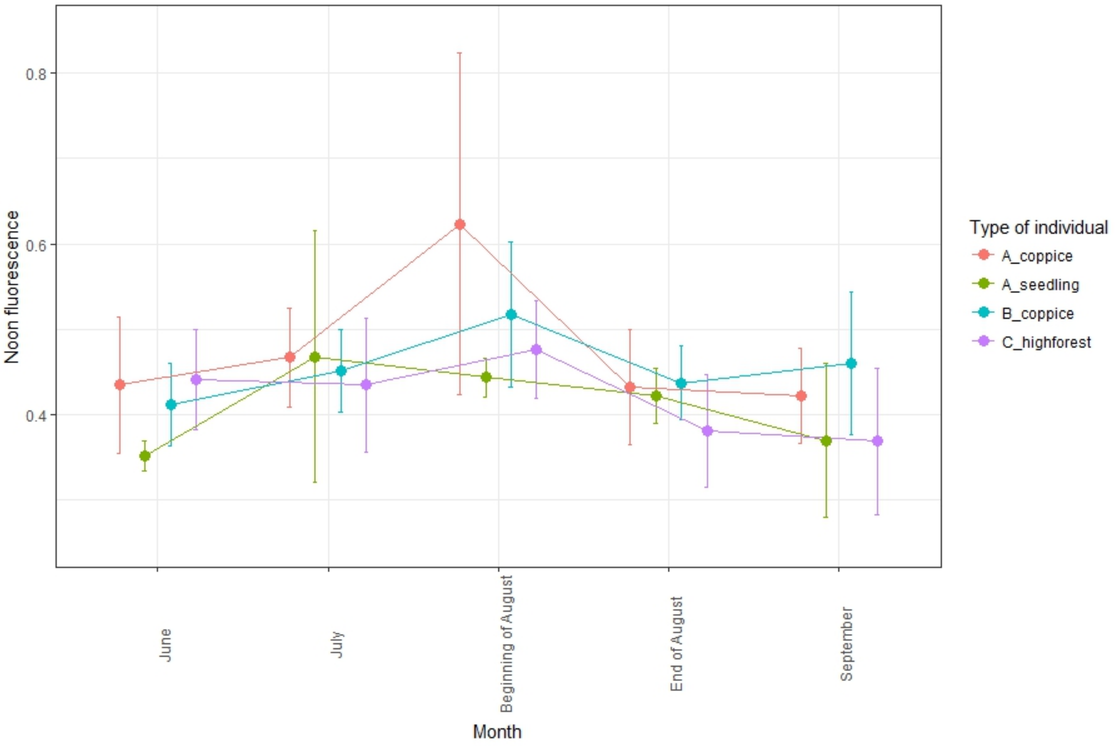

Figure 11: Plotted results of ANOVA showing differences of noon fluorescence between variants of experiment.

Simultaneous tests for multiple hypothesis have shown only one significant variability during testing predawn fluorescence, variability between A_seedling and C_high forest (p = 0.008) in June (Tab. 8, Fig. 12).

*Table 8: Significance of differences between variants in variable quantum yield. Significant codes for p-value: 0 < '***' < 0.001 < '**' < 0.01 < '*' < 0.05.*

Month	Interactions	p-value	Significance
June	C_highforest - A_seedling	0.00835	**

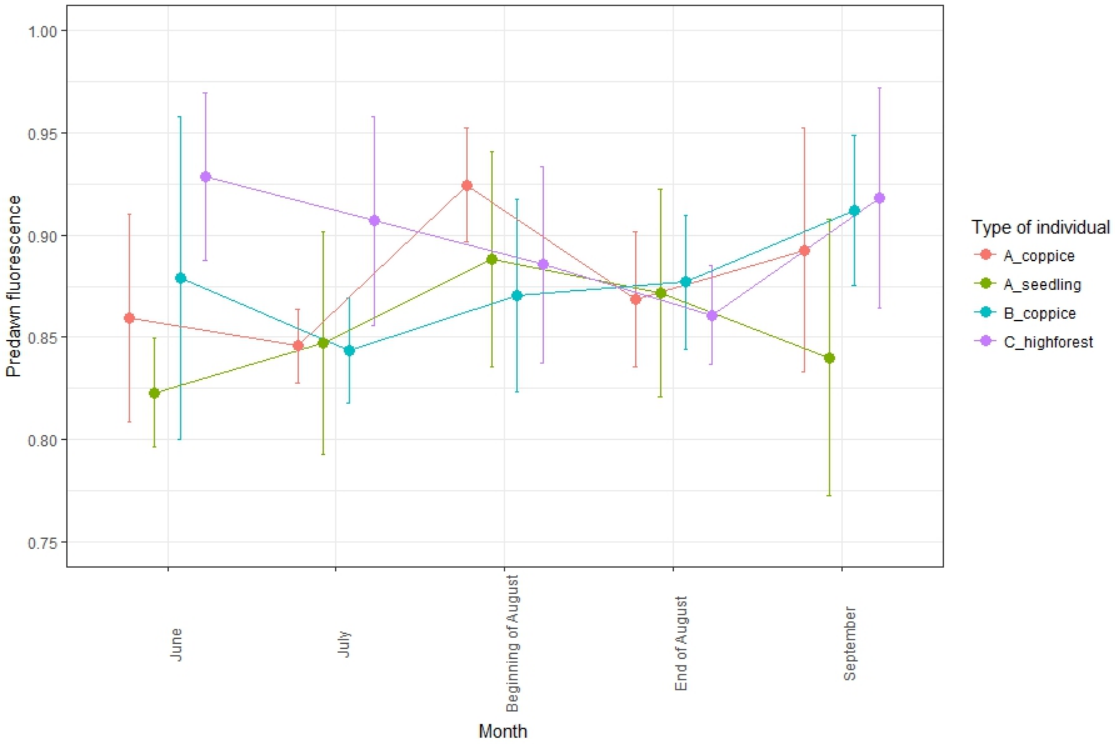

Figure 12: Plotted results of ANOVA showing differences of predawn fluorescence between variants of experiment.

5.5 *A*-*C*i curves

Measuring the relation how photosynthesis responds to changing CO_2 concentration using fitting photosynthetic carbon dioxide response curves showed differences in V_{cmax}, *J*, *TPU*, R_d and g_m among investigated variants of presented experiment (Tab. 9). The highest value of maximum carboxylation rate was found for C_highforest (75.5 µmol m^{-2} s^{-1}), followed by B_coppice (67.5 µmol m^{-2} s^{-1}), A_coppice (57.6 µmol m^{-2} s^{-1}) and finally A_seedling (41.2 µmol m^{-2} s^{-1}). The *J* and R_d showed the same trend as V_{cmax} – highest values in case of C_highforest (*J* = 140.5 µmol m^{-2} s^{-1}; R_d = 2.9 µmol m^{-2} s^{-1}) and lowest in case of A_seedling (*J* = 45.0 µmol m^{-2} s^{-1}; R_d = 1.5 µmol m^{-2} s^{-1}). The highest value of *TPU* and g_m was found in B_coppice (*TPU* = 6.4 µmol m^{-2} s^{-1}; g_m = 23.3 µmol m^{-2} s^{-1}), whereas the lowest value of both variables were found in case of A_seedling.

Since measurement was performed during several days, each tree was measured in another temperature. Variant A_coppice was measured in average temperature of 32.3 °C, B_coppice in average temperature of 29.6 °C, A_seedling was measured in 32.2 °C and 26.7 °C was the average temperature during measuring of C_highforest. Data was standardized to 25 °C.

Table 9: Table showing results of fitting photosynthetic carbon dioxide response curves with averaged values (AVG) standardized to 25 °C and standard deviations (SD) for all variants.

	A_coppice		**B_coppice**		**A_seedling**		**C_highforest**	
	AVG (25 °C)	**SD (25 °C)**	**AVG (25 °C)**	**SD (25 °C)**	**AVG (25 °C)**	**SD (25 °C)**	**AVG (25 °C)**	**SD (25 °C)**
V_{cmax} (μmol m^{-2} s^{-1})	57.611	18.750	67.467	14.424	41.156	26.342	75.466	18.610
J (μmol m^{-2} s^{-1})	72.392	31.655	88.057	28.700	45.029	29.984	140.521	60.816
TPU (μmol m^{-2} s^{-1})	5.966	2.023	6.381	1.231	4.437	2.455	5.841	1.868
R_d (μmol m^{-2} s^{-1})	1.889	0.596	2.351	0.282	1.481	1.140	2.890	0.500
g_m (μmol m^{-2} s^{-1} Pa^{-1})	19.340	2.083	23.344	7.013	12.689	9.390	21.162	18.157

5.6 Light curves

Using the Excel spreadsheet presented by Lobo et al. (2013) was employed the best fitting light-response curve (Equation 1) for current measured data by comparing sum of standard errors of all presented mathematical models. Fitting net photosynthetic light-response curves showed noticeably significant differences among variants of this experiment (Tab. 10, Fig. 13). In the first phase of light curves, where is a rapid increase in photosynthesis with increasing light from complete dark due to the natural decrease in dark respiration, known as Kok effect (Lobo et al. 2013), were not found significant differences between variants. For nearly all light intensities B_coppice had the highest values of *A*. The difference was significant in light intensity between 200 and 500 μmol m^{-2} s^{-1}. The lowest values of *A* at high intensities of radiation had the C_highforest, albeit not significantly.

Table 10: Results of fitting net photosynthetic light-response curves showed as averages of A for all variants and all investigated light intensities (PAR).

PAR (µmol m^{-2} s^{-1})	A_coppice *A* (µmol m^{-2} s^{-1})	B_coppice *A* (µmol m^{-2} s^{-1})	A_seedling *A* (µmol m^{-2} s^{-1})	C_highforest *A* (µmol m^{-2} s^{-1})
1500	12.17137	11.86587	11.02296	8.948807
1000	10.35176	12.3627	9.872542	8.436896
500	9.106301	11.59939	8.768359	7.828204
200	4.889139	8.04002	5.821784	5.911075
100	2.589175	4.180683	3.079222	3.297776
50	0.939378	2.631131	1.637581	1.779399
20	-0.44488	0.563751	1.827299	0.056942
0	-1.66728	-0.78135	-2.01452	-1.4848

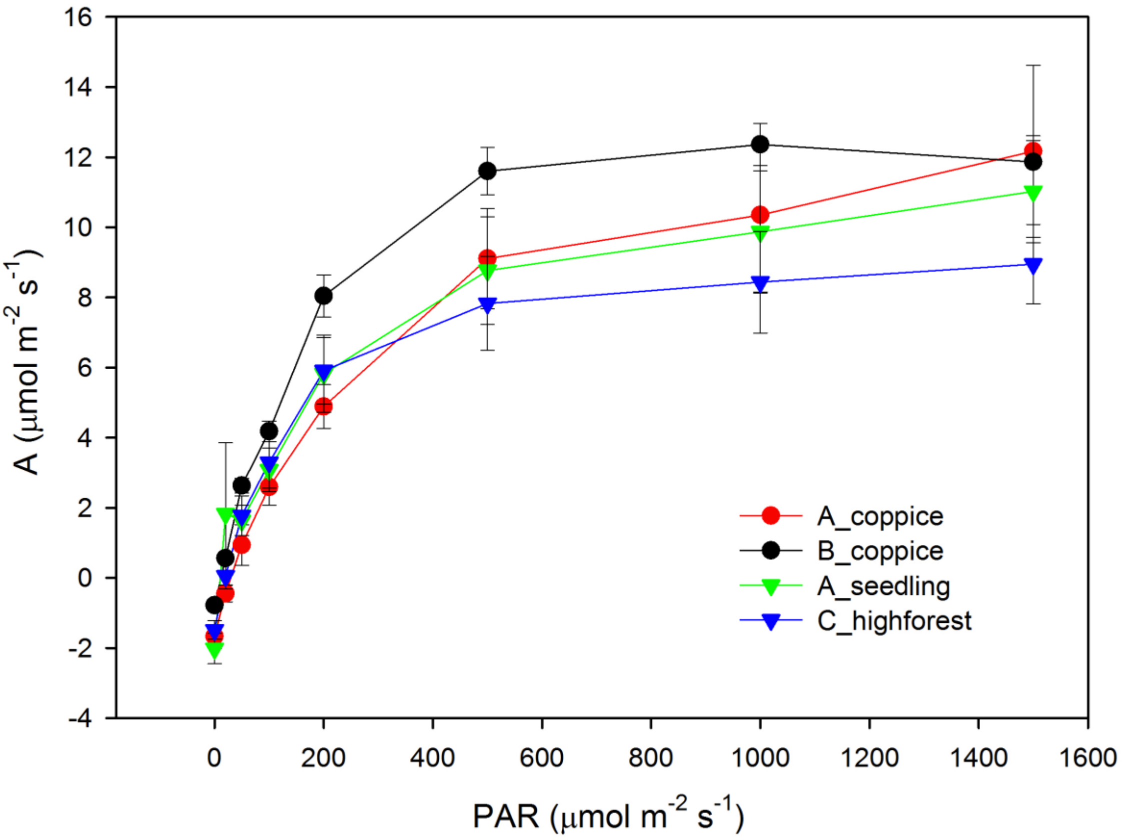

Figure 13: Light-response curves for all investigated variants.

I_{comp} little differed among variants. I_{comp} was highest in A_coppice 29.72±6.4 mmol (photons) m^{-2} s^{-1} and A_seedling 29.12±6.4 mmol (photons) m^{-2} s^{-1} while the C_highforest had I_{comp} of 23.43±8.7 mmol (photons) m^{-2} s^{-1}, and the lowest value was in case of B_coppice with the value of 11.72±0.5 mmol (photons) m^{-2} s^{-1} (Tab. 11).

Table 11: Table of light compensation points (I_{comp}), 50% light saturation points ($I_{sat(50)}$) and maximum saturation points (I_{max}) with standard errors (SD) for all variants.

Type of individual	I_{comp} (mmol (photons) m^{-2} s^{-1})	SD	$I_{sat(50)}$ (mmol (photons) m^{-2} s^{-1})	SD	I_{max} (mmol (photons) m^{-2} s^{-1})	SD
A_coppice	29.719	6.396	318.973	79.766	177.000	46.614
B_coppice	11.723	0.509	173.152	5.364	164.250	9.393
A_seedling	29.206	6.394	238.120	33.404	148.800	24.291
C_highforest	23.428	8.725	174.087	29.475	115.600	16.928

5.7 Leaf mass per area

The highest average value of LMA for the variant is in the case of A_coppice (91.1±7.4 m^2) whereas the lowest average value is in the case of A_seedlings (68.1±2.7 m^2) (Tab. 12).

Table 12: Averages of LMA for variant with standard errors.

Variant	Average of LMA [m^2]	Standard error of LMA
A_coppice	91.129	7.366
B_coppice	77.024	2.457
A_seedling	68.089	2.679
C_highforest	76.559	7.366

6 DISCUSSION

Coppice forest is in many ways different from the high forest. In this work I present several underlying ecophysiological mechanisms, which may result in difference in growth rates, health and survival of extreme events. Coppice trees were superior to high forest under water stress. They maintained higher water potentials which resulted in higher stomatal conductance and higher rates of photosynthesis. Coppicing also affected the environment which is in this work presented by differences in soil moisture.

The highest values of predawn and noon Ψ_w were found in A_coppice in June (Fig. 5, Tab. 2), which showed us the variant with the best water access and in case of noon Ψ_w also with connection to stomatal reduction. Contrastingly, the lowest values of Ψ_w were in A_seedling in September (Fig. 5, Supplementary table 1), respectively. It suggests that A_seedling suffered the most under the moderate drought conditions at the end of the vegetation season. Furthermore, A, g_s and Φ_{PSII} showed the same trend during the vegetation season, all of them confirmed the worst soil water conditions in September. All this variables are closely connected. When the soil moisture is insufficient the Ψ_w is decreasing and it is followed by stomata closure and coincidently it negatively affected g_s. Consequently, the A and Φ_{PSII} decreased too.

The plants do not have any mechanisms to affect predawn Ψ_w, thus the measured values showed current water availability for different variants. During the increasing dryness it is more complicated for roots to reach water, which can affect the trees health condition and physiological processes. Predawn Ψ_w measured in July showed the differences during moderate drought conditions. A_seedling and C_highforest had lowest water accessibility (Supplementary table 2, Fig. 6). Pietras et al. (2016) suggested that sprouts are less stressed by water limitation since they benefit from resources of sugars, starch, nutrients and others (Wildy and Pate 2002) stored in stumps of parent trees, which is noticeable even in July on A_coppice and B_coppice (Fig. 6). On the other hand, plants are able to influence value of noon Ψ_w by regulating stomata according to actual weather conditions. Plants tend to reduce stomata opening under water stress to maximize water use efficiency (Lambers et al. 2008). Regulation of stomata in changing weather conditions and efforts to preserve similar values of Ψ_w to protect vessels against cavitation are closely adherent also to g_s (Collatz et al. 1991), which is noticeable also from presented results. When Ψ_w decreased the g_s (and photosynthesis) decreased too (Fig. 7 and Fig. 9). Stomata structure functions to restrict water loss from the photosynthetic cells of the leaf mesophyll, nevertheless they must also permit CO_2 to diffuse into the leaf to support photosynthesis (Collatz et al. 1991). Orság et al. (2012) measured g_s based on meteorological variables on poplars. He proved that g_s moderately responds to soil moisture availability, but strongly responds to VPD, which explains why in time of higher VPD are trees effectively regulating their transpiration by stomata closing. As mentioned above,in this thesis was also supported clear correlation between g_s and soil moisture availability with connection to photosynthesis.

The highest *A* was again in A_coppice but at the beginning of August not in June. At the beginning of August was not big absence of soil water caused by very rainy period in July. The lowest value confirmed again the worst water availability in A_seedling in September (Supplementary table 3). Furthermore, *A* and g_s showed strong correlation (Fig. 8) during the whole vegetation season. Carbon dioxide response curves showed the highest V_{Cmax} in C_highforest and lowest in A_seedling (Tab. 9), which suggest highest Rubisco activity. The *J* and R_d showed the same trend as V_{cmax}. Light response curves showed significant differences especially in I_{comp}, when the highest value of I_{comp} was in A_coppice (29.72±6.4 mmol (photons) m^{-2} s^{-1}) and A_seedling (29.12±6.4 mmol (photons) m^{-2} s^{-1}), while the lowest was in B_coppice (11.72±0.5 mmol (photons) m^{-2} s^{-1}). Generally, all measured variables showed correlation with weather conditions and with the leaf age at the end of season.

A showed clear correlation with g_s and Ψ_w which support relation mentioned above. For instance in June it was low value of both, *A* and g_s, especially in case of A_seedling, which closed stomata because of drought stress (Table 5, Fig. 9). It is often seen that leaf conductance decreases with any factor decreasing photosynthesis (Long and Bernacchi 2003). Steppe et al. (2011) asserts that g_s usually declines with the tree height and age, due to longer hydraulic pathways and increase in the leaf-area-to-sapwood-area ratio. It can be one of the reasons, why C_highforest had one of the lowest g_s during the whole season. Similarly they behaved in July, but during this time also with C_highforest – consequently they closed stomata to reduce water stress. Important fact is also the g_m, which changes the relation between *A* and g_s, because it acts like limiting factor for CO_2 diffusion into the leaf and by this lowers g_s (Pons et al. 2009). Nevertheless, at the beginning of August all variants showed similar results of Φ_{PSII}, only the C_highforest had lower values. It is reflecting some problems in light-dependent parts of photosynthesis, because values of Ψ_w are similar to values for other variants.

In spite of that, predawn fluorescence of C_highforest is analogous to values of other variants and explaining that the problem is not the leaf damage but some photo-protective plant function. At the end of August C_highforest had lowest A which this time correlates with lower values of Ψ_w. In any case this showed worse availability of water for this variant which results in decreased A. Holišová et al. (2016) claimed, that a higher g_s allow sprouts to maintain a higher rate of assimilates use. The same trend is supported also by this work. However, photosynthetic capacity is also affected by air temperature (Flexas et al. 2014) and August of 2016 was really warm, which might be negatively affecting results. According to Collatz et al. (1991) is also approved that midday stomata closure can be driven by excessively high leaf temperature (at low values of leaf boundary-layer conductance (g_b)) and by drying of the air at the surface of the leaf (at high values of g_b).

Response of net photosynthesis to CO_2 revealed higher V_{cmax} rate in C_highforest than in coppice (Tab. 9), but low g_s was the reason, why C_highforest had low values of A. The strength of stress caused by drought can be read also from A-C_i response curves. When only the conductance declines with plant desiccation, the curve slope is unaffected (Lambers et al. 2008). However, compared with this statement experimented individuals were exposed to more strong drought conditions, because curve slope was very small. The decline of photosynthetic capacity in water-stressed plants is associated in all biochemical components of photosynthesis (Lambers et al. 2008). Spreitzer and Salvucci (2002) mentioned that a temperature is very important variable during observation of A-C_i relation because above 35 °C may occur a further loss of activation affecting on Rubisco activase. Almost all A-C_i curves were measured in high temperatures around or even above 30 °C so the V_{cmax} and activation of Rubisco can be negatively influenced. Collatz et al. (1991) showed simulations indicating that the conductance of a leaf boundary layer can have significant influences on the canopy response properties. Anyway, g_b was kept by the LI-6400 all the time at the same level. Fortunately, the response of A to C_i eliminates the effect of boundary layer and stomata, it depends solely on mesophyll processes. A drop of C_i below ambient concentration lower A and the pools of Calvin cycle intermediates, which can also affect the activity of Rubisco and other enzymes (Long and Bernacchi 2003).

Light compensation point little differed among variants. The lowest value was found in case of B_coppice, then followed C_highforest, and next A_seedling and A_coppice had very similar values. It showed, that B_coppice compensated respiratory carbon loss like the first one variant. Whilst A_coppice showed the highest light saturated net photosynthesis results, C_highforest was the most carboxylation-limited from all the variants, probably as a result of low stomatal conductance since they had highest carboxylation capacity (Lambers et al. 2008).

The differences in leaf mass area among the variants of this experiment can correlate with the amount of the nitrogen (Jullien et al. 2009), RuBisCO and photosynthetic capacity. The biggest LMA was found in A_coppice. Accordingly, here can be seen the relationship with the highest A, g_s and water availability because this variant is able to invest the biggest amount of energy into the growth, which is proved by the LMA results. Furthermore, this variable acts as a function of light (Aranda et al. 2004). Plasticity of LMA may also be related to age and tree position in canopy (Richardson et al. 2000) or to nutrient availability. A_seedling is the youngest variant, while the C_highforest are the oldest one. Age could explain why measured seedlings have the lowest average value of LMA, on their smallest and also youngest leaves, whereas A_coppice, with the biggest leaves, have the highest value of LMA. Amount of nitrogen nutrients availability was not tested during this experiment. Reich et al. (1991) conclude that LMA is plastic with respect to micro-environmental factors (light, nutrients, etc.), which differ for all variants of this experiment.

In September the lowest results in all variables and also all variants were found, which might be caused not only by drought but in addition by the end of vegetation period (Reich et al. 1991). If the stress becomes more severe the plant is no longer able to maintain balance between water uptake and loss (Verslues et al. 2006). Reich et al. (1991) found also the relation between leaf age, photosynthesis, LMA and leaf nitrogen – at the leaf senescence (October) are all these variables declining. Holland et al. (2016) found changes in chlorophyll fluorescence under drought stress conditions. However, this experiment did not show any interesting significant differences in chlorophyll fluorescence measurement, except the one mentioned above connected with photo-protective function.

It also cannot be forgotten that variant C_highforest consists of approximately 80 years old trees. It is not too much for *Q. petraea*, but on the other hand it can play a key role in comparing physiological functions with younger individuals. Age differences are more perceptible even in comparing with approximately 8 year old sprouting coppiced or seedlings of vegetative origin. Another elemental fact is that measured trees from C_highforest were used to growth dense canopy closure for many years but with the setting up the experimental plot they became boundary trees. Because of it C_highforest suffered top crown dieback.

Variance was also found among individual trees within each variant. The highest variance was found in A_coppice, while the lowest in C_highforest. It indicates bigger differences within all measured variables and also the higher values of standard errors. High forest is more uniform in a lot of parameters, e.g. in height or diameters, also there are low fluctuations even in *A*.

Results of Holišová et al. (2016) did not show higher photosynthetic activity of coppice following their faster above-ground development compared with seedlings investing more into the root biomass. She found differences also only under the drought stress conditions. She claim that during the moderate water deficit the main cause for decreased photosynthesis is the decreased diffusion of CO_2 due to stomatal closure. Pietras et al. (2016) supported same hypothesis, when she found differences in transpiration occurring when soil water potential dropped below -1.4 MPa.

Further studies attended in studying amounts of non-soluble sugars and amount of carbon in leaves and roots might lead into the deeper understanding of physiological processes connected with photosynthesis and assimilation and also with the starting growing rates of the coppice. It is very important to linked all variables with the weather measurements and create predictions. Žalud (2008) presented methodology to evaluate drought periods in the region of the Czech Republic, software SoilClim and analysis of vulnerability and sustainability of ecosystems in conditions of global change. Fast climate change can decrease the stability of agriculture and forest ecosystems, including soil ecology. Consequently it will change the amount of soil microbes and their activity, erodibility, compaction, infiltration capacity and salinity. It may be very useful to connect ecosystems sustainability with coppice management.

As proved by many authors (Sakai and Sakai 1998; Bond and Midgley 2001; Lloret et al. 2004; Drake et al. 2009; Holišová et al. 2016; Pietras et al. 2016) coppice better cooperate their physiological functions during drought periods thanks to their larger existing systems. This study support same hypothesis because in almost every measured physiological function had coppices the best results, even under drought stress. From not only physiological point of view is the coppice good alternative forest management for the future and sites with insufficient water availability connected with climate changes.

7 CONCLUSION

Coppice and high forest, differing in their regeneration form, showed a great divergence in many ecophysiological mechanisms. When the soil water was not limiting factor both, coppice and high forest, behaved similarly. However, coppice forest was significantly superior to high forest in behaviour under water stress. It showed better coping with water supply using previously developed root system by maintaining higher water potential due insufficient soil water availability. Higher values of water potential lead to the higher stomatal conductance and quantum yield of photosynthesis, which allowed to keep higher rates of photosynthesis compared to values of high forest. Rates of photosynthesis enables to invest the most energy into the growth. Nevertheless, response of net photosynthesis to CO_2 concentration revealed higher carboxylation rates in high forest than in coppice. On the other hand, low stomatal conductance was a reason for overall lower photosynthetic rates in high forest than in coppice.

This study showed, that coppice are the most drought tolerant way of forest management and thus may be a proper solution for the future and climate change.

8 SUMMARY

Tématem předložené diplomové práce je problematika rozdílu fotosyntézy a vodního provozu dubu zimního (*Quercus petraea* (Matt.) Liebl.). Sběr dat se uskutečnil na výzkumné ploše v Soběšicích v roce 2016. Zkoumaná plocha se nachází na polesí Vranov Školního lesního podniku Křtiny, speciálního výukového území Mendelovy univerzity v Brně. Porovnány byly tři hospodářské způsoby – nízký, střední a vysoký les ve dvou variantách (semenáčky a kmenovina). V každé variantě bylo vybráno 6 jedinců, na kterých probíhalo pravidelné ekofyziologicky zaměřené měření. Na úrovni listů byl měřen vodní potenciál, průduchová vodivost, chlorofylová fluorescence, plošná hustota listoví, fotosyntéza a její reakce na různé intenzity světla, formou světelných křivek, a různé koncentrace CO_2, formou *A*-*C*$_i$ křivek. Výsledky měření byly poté srovnány s meteorologickými záznamy a hodnotami půdní vlhkosti, které ukázaly, že měření jedinci byli během sezóny vystaveni mírnému stresu suchem. Za nelimitujícího obsahu vody v půdě nebyly objeveny žádné významné rozdíly mezi jednotlivými variantami výzkumu. Jakmile byli jedinci stresovaní, začali se od sebe skupiny významně lišit, nicméně nízký les projevil vyšší odolnost vůči stresu suchem, než les vysoký. Projevilo se to vyšší hodnotou stomatální vodivosti a kvantového výtěžku fotosyntézy, což nízkému lesu umožnilo i vyšší rychlost fotosyntézy. Nejnižší hodnota vodního potenciálu měřeného před rozbřeskem byla u vysokého lesa, zatímco nejvyšší byla v lese nízkém. Nejvyšší hodnota vodního potenciálu naměřená u nízkého lesa indikuje lepší přístupnost výmladků k vodě v půdě díky rozdílům v kořenovém systému a nižší evapotranspiraci, která byla pravděpodobně způsobena celkově nižší aerodynamickou vodivostí nízkého lesa. Reakce fotosyntézy na změny koncentrací CO_2 odhalila vyšší rychlost karboxylace u vysokého lesa než u nízkého lesa, nicméně nízká stomatální vodivost vysokého lesa byla důvodem k celkově nižší rychlosti fotosyntézy, než tomu bylo u nízkého lesa. Schopnost nízkého lesa odolávat suchu jej předurčuje jako vhodnou alternativu lesního hospodaření na vysychavých lokalitách v procesu globálních klimatických změn.

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9.1 Online sources

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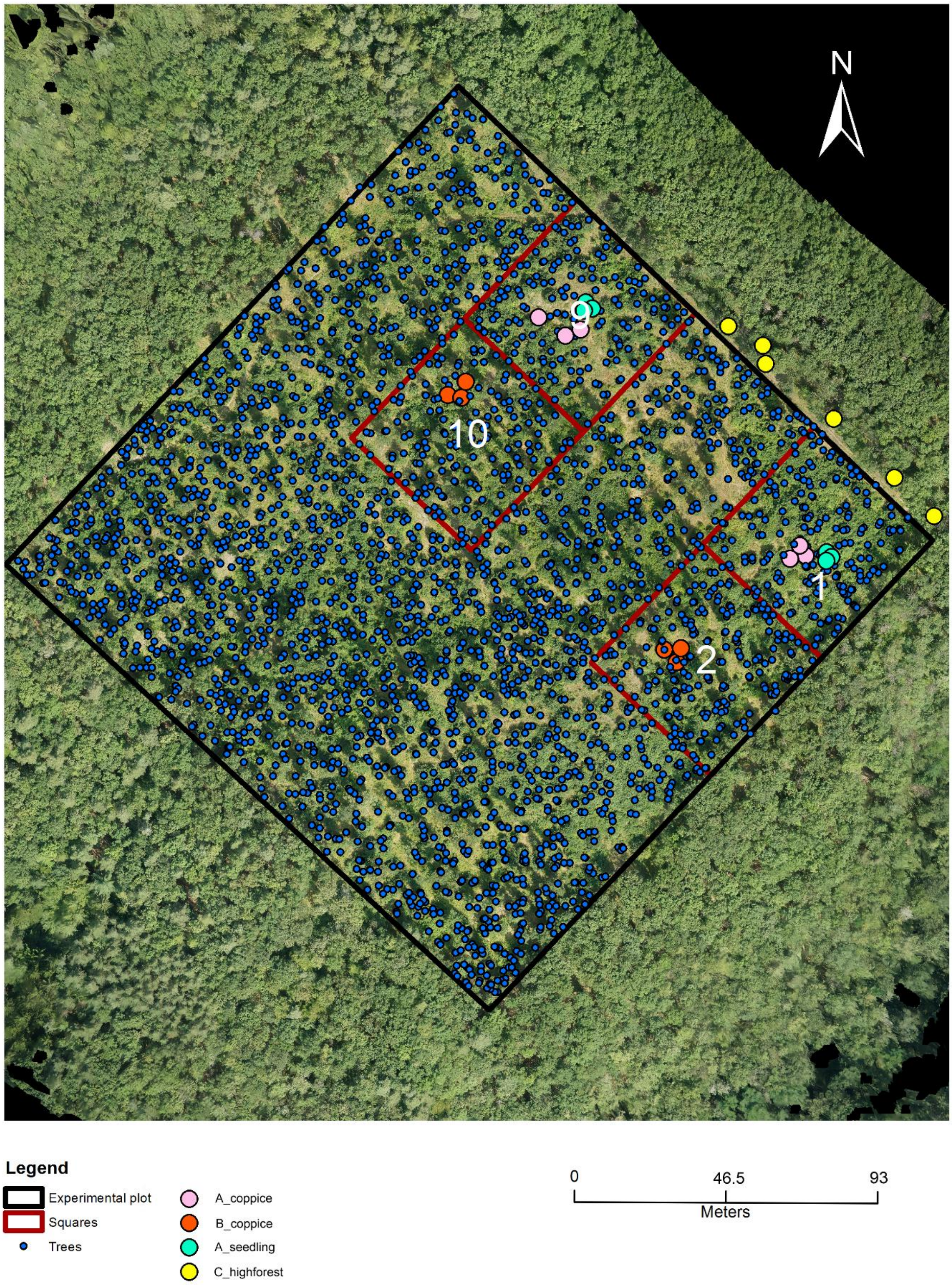
9.2 List of tables

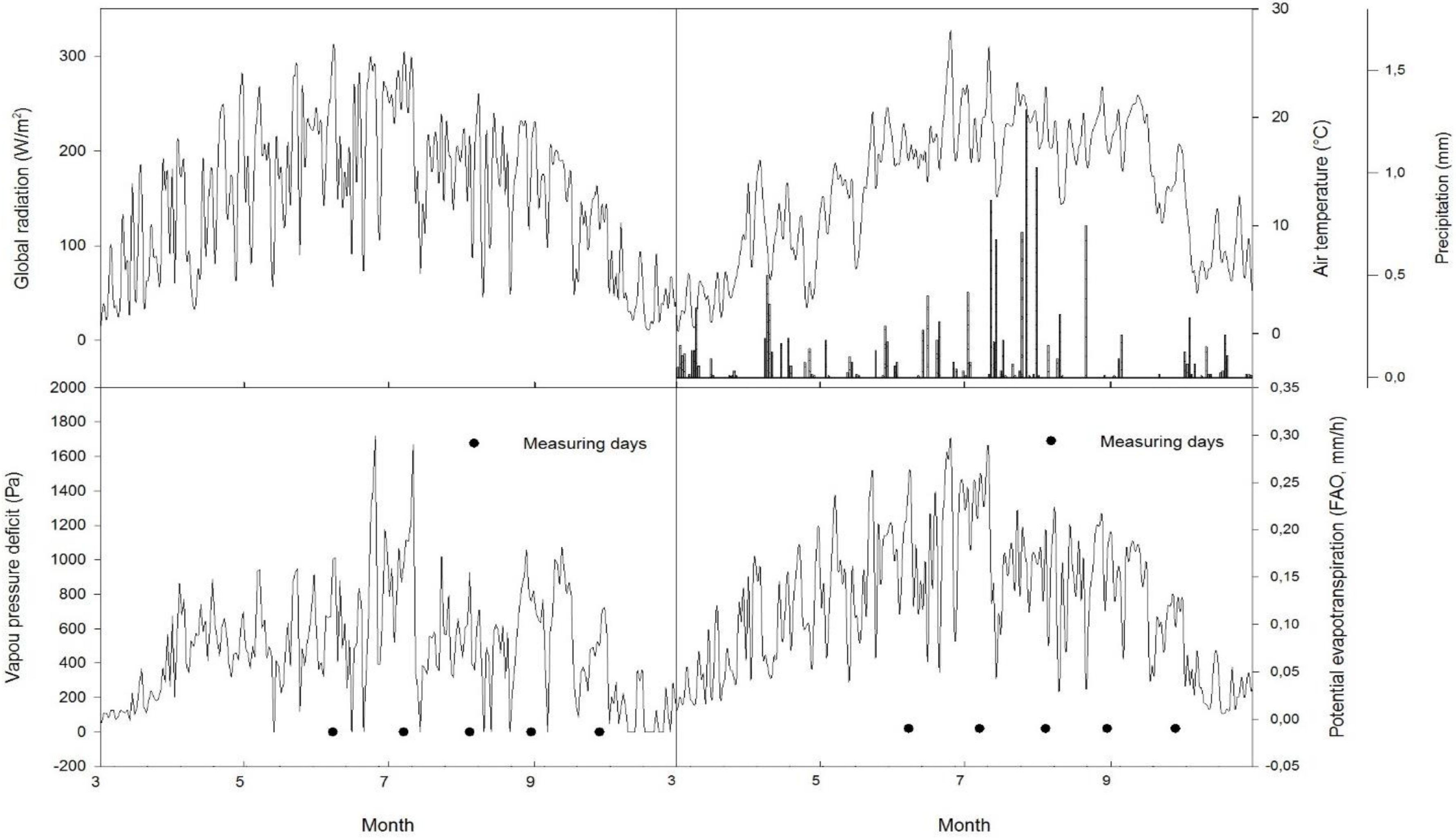
9.3 List of figures

10 APPENDIX

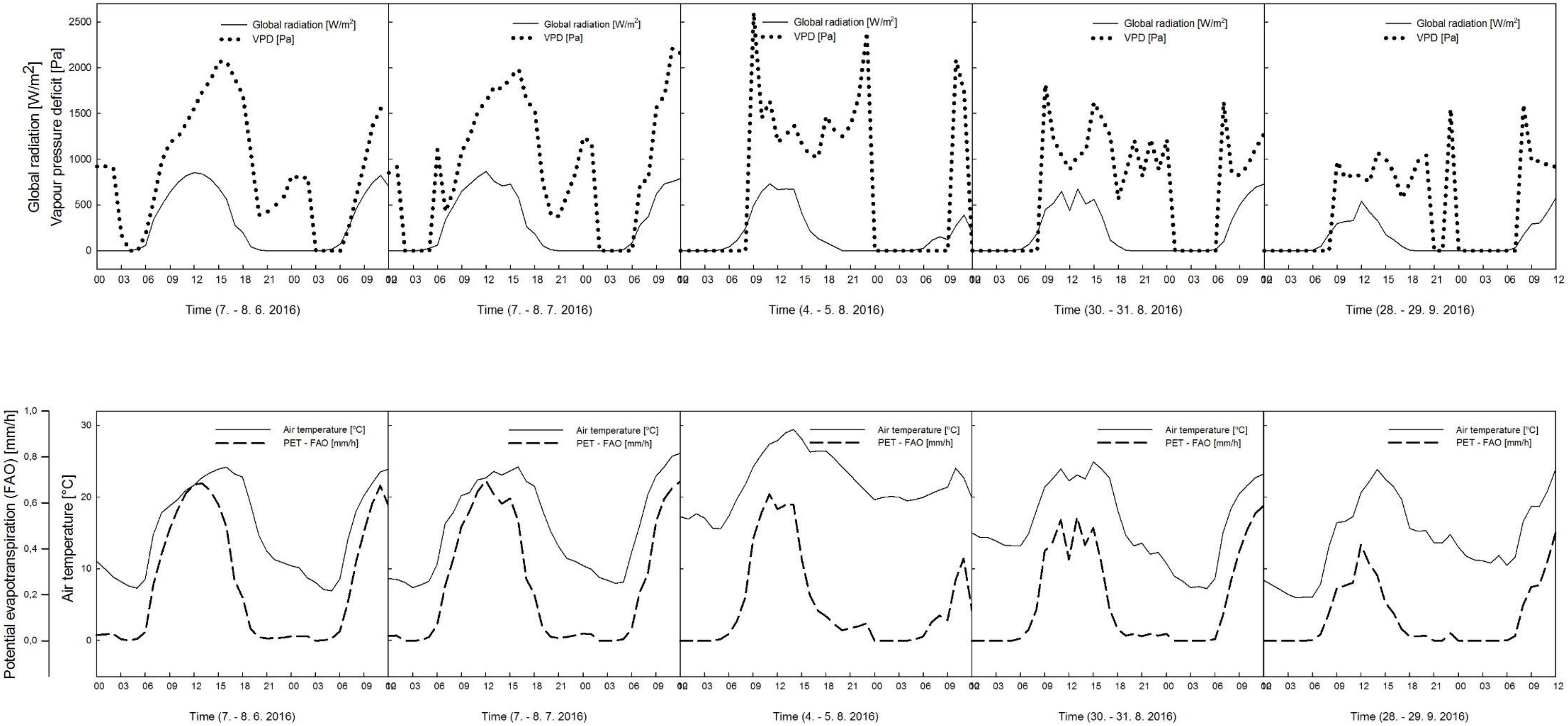
10.1 List of supplements



Supplementary figure 1: Map of experimental plot with boundary, squares 1, 2, 9, 10, all the trees on the experimental plot, A_coppice, B_coppice, A_seedling and C_highforest displayed.



Supplementary figure 2: Evolution of climatic variables during the vegetation season of 2016 with displayed measuring days.



Supplementary figure 3: Detailed weather conditions during measuring days, from midnight of the first day till the noon of the second day.

Supplementary table 1: Noon water potential for all examined variants with averages for each month with standard deviation, standard error and confidence intervals.

Type of individual	**Month**	**Noon water potential [Mpa]**	**Standard deviation**	**Standard error**	**Confidence interval (+/-)**
A_coppice	June	-1.308	0.252	0.103	0.264
A_coppice	July	-2.175	0.094	0.038	0.098
A_coppice	Beginning of August	-2.067	0.250	0.102	0.263
A_coppice	End of August	-2.567	0.082	0.033	0.086
A_coppice	September	-3.325	0.496	0.202	0.520
A_seedling	June	-1.542	0.183	0.075	0.192
A_seedling	July	-2.629	0.202	0.076	0.187
A_seedling	Beginning of August	-2.050	0.208	0.079	0.193
A_seedling	End of August	-2.407	0.270	0.102	0.250
A_seedling	September	-3.936	0.270	0.102	0.250
B_coppice	June	-1.717	0.260	0.106	0.273
B_coppice	July	-2.342	0.136	0.055	0.142
B_coppice	Beginning of August	-1.992	0.289	0.118	0.303
B_coppice	End of August	-2.567	0.175	0.071	0.184
B_coppice	September	-3.333	0.154	0.063	0.161
C_highforest	June	-1.933	0.194	0.079	0.204
C_highforest	July	-2.442	0.136	0.055	0.142
C_highforest	Beginning of August	-2.183	0.477	0.195	0.501
C_highforest	End of August	-2.833	0.061	0.025	0.064
C_highforest	September	-3.592	0.166	0.068	0.174

Supplementary table 2: Predawn water potential for all examined variants with averages values for each month with standard deviation, standard error and confidence intervals.

Type of individual	Month	Predawn water potential [MPa]	Standard deviation	Standard error	Confidence interval (+/-)
A_coppice	June	-0.242	0.020	0.008	0.021
A_coppice	July	-0.550	0.293	0.120	0.308
A_coppice	Beginning of August	-0.367	0.246	0.101	0.258
A_coppice	End of August	-0.900	0.339	0.138	0.356
A_coppice	September	-2.033	0.856	0.349	0.898
A_seedling	June	-0.408	0.080	0.033	0.084
A_seedling	July	-1.429	0.283	0.107	0.261
A_seedling	Beginning of August	-0.229	0.076	0.029	0.070
A_seedling	End of August	-1.114	0.366	0.138	0.338
A_seedling	September	-2.371	0.834	0.315	0.771
B_coppice	June	-0.317	0.098	0.040	0.103
B_coppice	July	-0.700	0.228	0.093	0.239
B_coppice	Beginning of August	-0.433	0.121	0.049	0.127
B_coppice	End of August	-1.458	0.196	0.080	0.206
B_coppice	September	-2.633	0.246	0.101	0.258
C_highforest	June	-0.317	0.103	0.042	0.108
C_highforest	July	-1.458	0.208	0.085	0.219
C_highforest	Beginning of August	-0.517	0.088	0.036	0.092
C_highforest	End of August	-2.017	0.166	0.068	0.175
C_highforest	September	-3.267	0.178	0.073	0.187

Supplementary table 3: Photosynthesis for all examined variants with averages values for each month with standard deviation, standard error and confidence intervals.

Type of individual	**Month**	**Photosynthesis [µmol m^{-2} s^{-1}]**	**Standard deviation**	**Standard error**	**Confidence interval (+/-)**
A_coppice	June	13.648	4.629	1.890	4.858
A_coppice	July	9.026	3.802	1.552	3.990
A_coppice	Beginning of August	15.085	4.917	2.007	5.160
A_coppice	End of August	9.406	5.192	2.119	5.448
A_coppice	September	2.463	0.630	0.282	0.782
A_seedling	June	4.841	1.189	0.485	1.248
A_seedling	July	4.451	1.912	0.723	1.768
A_seedling	Beginning of August	12.333	2.972	1.123	2.749
A_seedling	End of August	7.778	2.404	0.909	2.223
A_seedling	September	0.864	0.513	0.209	0.538
B_coppice	June	10.148	6.407	2.615	6.723
B_coppice	July	8.743	3.627	1.481	3.806
B_coppice	Beginning of August	13.804	5.619	2.294	5.897
B_coppice	End of August	7.022	2.709	1.106	2.843
B_coppice	September	2.488	2.305	0.941	2.419
C_highforest	June	12.236	2.331	0.951	2.446
C_highforest	July	4.517	1.231	0.503	1.292
C_highforest	Beginning of August	7.291	1.553	0.634	1.630
C_highforest	End of August	2.221	0.743	0.303	0.779
C_highforest	September	2.271	1.597	0.652	1.676

Supplementary table 4: Conductance for all examined variants with averages values for each month with standard deviation, standard error and confidence intervals.

Type of individual	**Month**	**Conductance [mmol m^{-2} s^{-1}]**	**Standard deviation**	**Standard error**	**Confidence interval (+/-)**
A_coppice	June	0.137	0.047	0.019	0.049
A_coppice	July	0.083	0.052	0.021	0.055
A_coppice	Beginning of August	0.221	0.082	0.034	0.086
A_coppice	End of August	0.094	0.069	0.028	0.072
A_coppice	September	0.026	0.002	0.001	0.003
A_seedling	June	0.044	0.011	0.004	0.011
A_seedling	July	0.031	0.015	0.006	0.014
A_seedling	Beginning of August	0.186	0.053	0.020	0.049
A_seedling	End of August	0.078	0.036	0.014	0.033
A_seedling	September	0.016	0.007	0.003	0.007
B_coppice	June	0.121	0.083	0.034	0.087
B_coppice	July	0.078	0.043	0.018	0.045
B_coppice	Beginning of August	0.194	0.042	0.017	0.044
B_coppice	End of August	0.057	0.023	0.010	0.025
B_coppice	September	0.051	0.046	0.023	0.073
C_highforest	June	0.114	0.026	0.010	0.027
C_highforest	July	0.041	0.018	0.007	0.019
C_highforest	Beginning of August	0.094	0.024	0.010	0.025
C_highforest	End of August	0.014	0.006	0.002	0.006
C_highforest	September	0.003	0.001	0.001	0.003

Supplementary table 5: Quantum yield for all examined variants with averages values for each month with standard deviation, standard error and confidence intervals.

Type of individual	**Month**	**Quantum yield**	**Standard deviation**	**Standard error**	**Confidence interval (+/-)**
A_coppice	June	0.229	0.044	0.018	0.047
A_coppice	July	0.189	0.051	0.021	0.053
A_coppice	Beginning of August	0.267	0.020	0.008	0.021
A_coppice	End of August	0.218	0.045	0.018	0.047
A_coppice	September	0.162	0.062	0.025	0.065
A_seedling	June	0.162	0.023	0.009	0.024
A_seedling	July	0.129	0.031	0.012	0.029
A_seedling	Beginning of August	0.236	0.032	0.013	0.034
A_seedling	End of August	0.162	0.039	0.015	0.036
A_seedling	September	0.074	0.015	0.006	0.014
B_coppice	June	0.202	0.043	0.018	0.045
B_coppice	July	0.162	0.054	0.022	0.057
B_coppice	Beginning of August	0.233	0.030	0.012	0.032
B_coppice	End of August	0.170	0.024	0.010	0.025
B_coppice	September	0.074	0.036	0.015	0.038
C_highforest	June	0.214	0.034	0.014	0.036
C_highforest	July	0.166	0.020	0.008	0.020
C_highforest	Beginning of August	0.175	0.026	0.012	0.033
C_highforest	End of August	0.115	0.022	0.009	0.023
C_highforest	September	0.073	0.014	0.006	0.014

Supplementary table 6: Noon fluorescence for all examined variants with averages values for each month with standard deviation, standard error and confidence intervals.

Type of individual	Month	Noon fluorescence	Standard deviation	Standard error	Confidence interval (+/-)
A_coppice	June	0.434	0.076	0.031	0.079
A_coppice	July	0.467	0.055	0.023	0.058
A_coppice	Beginning of August	0.623	0.191	0.078	0.200
A_coppice	End of August	0.433	0.064	0.026	0.068
A_coppice	September	0.422	0.053	0.022	0.056
A_seedling	June	0.351	0.017	0.007	0.018
A_seedling	July	0.467	0.160	0.060	0.148
A_seedling	Beginning of August	0.443	0.025	0.009	0.023
A_seedling	End of August	0.422	0.035	0.013	0.033
A_seedling	September	0.369	0.097	0.037	0.090
B_coppice	June	0.411	0.046	0.019	0.049
B_coppice	July	0.451	0.046	0.019	0.049
B_coppice	Beginning of August	0.517	0.081	0.033	0.085
B_coppice	End of August	0.437	0.041	0.017	0.043
B_coppice	September	0.460	0.080	0.033	0.084
C_highforest	June	0.440	0.056	0.023	0.059
C_highforest	July	0.434	0.075	0.031	0.079
C_highforest	Beginning of August	0.476	0.046	0.021	0.057
C_highforest	End of August	0.380	0.063	0.026	0.066
C_highforest	September	0.368	0.081	0.033	0.085

Supplementary table 7: Predawn fluorescence for all examined variants with averages values for each month with standard deviation, standard error and confidence intervals.

Type of individual	**Month**	**Predawn fluorescence**	**Standard deviation**	**Standard error**	**Confidence interval (+/-)**
A_coppice	June	0.859	0.048	0.020	0.051
A_coppice	July	0.846	0.017	0.007	0.018
A_coppice	Beginning of August	0.924	0.027	0.011	0.028
A_coppice	End of August	0.869	0.032	0.013	0.033
A_coppice	September	0.893	0.057	0.023	0.060
A_seedling	June	0.823	0.025	0.010	0.027
A_seedling	July	0.847	0.059	0.022	0.055
A_seedling	Beginning of August	0.888	0.057	0.021	0.053
A_seedling	End of August	0.872	0.055	0.021	0.051
A_seedling	September	0.840	0.073	0.028	0.068
B_coppice	June	0.879	0.075	0.031	0.079
B_coppice	July	0.843	0.025	0.010	0.026
B_coppice	Beginning of August	0.870	0.045	0.018	0.047
B_coppice	End of August	0.877	0.031	0.013	0.033
B_coppice	September	0.912	0.035	0.014	0.037
C_highforest	June	0.928	0.039	0.016	0.041
C_highforest	July	0.907	0.049	0.020	0.051
C_highforest	Beginning of August	0.886	0.046	0.019	0.048
C_highforest	End of August	0.861	0.023	0.009	0.024
C_highforest	September	0.918	0.051	0.021	0.054