



Agrometeorological aspects of growth and development of short rotation coppice

“Agrometeorologické aspekty růstu a vývoje rychle rostoucích dřevin”

Ph.D. thesis

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PROHLÁŠENÍ

Prohlašuji, že jsem disertační práci na téma „**Agrometeorologické aspekty růstu a vývoje rychle rostoucích dřevin**“ vypracoval samostatně a použil jen pramenů, které cituji a uvádím v příloženém seznamu literatury.

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CONTENTS

1	INTRODUCTION	9
1.1	Environment of Plants	9
1.1.1	Stress factors	9
1.1.2	Radiation	12
1.1.3	Temperature	12
1.1.4	Wind	13
1.1.5	Water and drought	14
1.2	Climate change	16
1.3	Drought assessment	17
1.3.1	Palmer drought severity index	18
1.3.2	Assesment of meteorological drought in studied area using Palmer drought indices	19
1.4	Short rotation coppice	22
1.4.1	Short rotation coppice in the Czech Republic	24
1.4.2	Poplar	24
2	AIMS	27
3	MATERIALS AND METHODS	28
3.1	Locality	28
3.2	Climate conditions	28
3.3	Poplar plantation	30
3.4	Experimental design	31
3.5	Soil water	32
3.5.1	Soil moisture	32
3.5.2	Soil water potential	33
4	CHAPTER I.: ANALYSIS OF DECREASED SOIL WATER AVAILABILITY ON ABOVE-GROUND BIOMASS PRODUCTIVITY	34
4.1	Methods	35
4.1.1	Above-ground biomass productivity	35
4.1.2	Analysis of dominance	37
4.2	Results	38
4.2.1	Soil moisture patterns and experimental design	38
4.2.2	Above ground biomass productivity	42
4.2.3	Analysis of dominance	44

4.3 Discussion	49
4.3.1 Soil moisture patterns and experimental design evaluation	49
4.3.2 Above-ground biomass productivity	52
4.3.3 Analysis of dominance	56
4.4 Conclusion	59
5 CHAPTER II.: ANALYSIS OF DECREASED SOIL WATER AVAILABILITY ON WATER USE	60
5.1 Introduction	60
5.1.1 Plant water relations	60
5.1.2 Sap flow	61
5.1.3 Transpiration	64
5.1.4 Water use efficiency	64
5.2 Methods	65
5.2.1 Sap flow	65
5.2.2 Water use efficiency	73
5.3 Results	74
5.3.2 Sap flow	80
5.3.3 Transpiration	83
5.3.4 Water use efficiency	96
5.4 Discussion	97
5.4.2 Sap flow	101
5.4.3 Transpiration	106
5.4.4 Water use efficiency	108
5.5 Conclusion	110
REFERENCES	111
APENDIXES	122
APPENDIX A: LIST OF ABBREVIATIONS AND SYMBOLS USED IN THE TEXT	122
APPENDIX B: LIST OF TABLES	123
APPENDIX C: LIST OF FIGURES	124
ANNOTATION	126

SOUHRN

Obnovitelné zdroje energie (OZE) jsou v současnosti stále častěji spojovány s udržitelným hospodářským růstem společnosti za cenu akceptovatelných dopadů na životní prostředí a emisí CO₂. V porovnání s konvenčními zdroji energie, OZE zpravidla vykazují CO₂ neutrální bilanci, v lepším případě CO₂ neemitují vůbec. Zároveň snižují závislost na dovozu fosilních paliv. I to je jeden z důvodů, pro které se Evropská unie rozhodla do roku 2020 zvýšit podíl OZE v energetice na 20 % a v dopravním sektoru na 10 %. Kromě solární energie je v podmínkách střední Evropy za vhodný zdroj OZE považována energie z biomasy. Kromě jednoletých plodin vhodných spíše k výrobě biopaliv má největší produkční potenciál pěstování rychle rostoucích dřevin (RRD) na orné půdě. Tyto dřeviny, nejčastěji kříženci topolů, případně vrb, jsou šlechtěny pro rychlý růst a jsou nejčastěji pěstovány ve formě hustě osázených plantáží. Mimo schopnost rychlé akumulace biomasy mají plantáže RRD významné pozitivní mimoprodukční a ekosystémové funkce. V posledních letech zažíváme rozmach RRD, kdy se pěstební výměra v České republice meziročně znásobovala.

S ohledem na probíhající klimatickou změnu lze v oblasti střední Evropy v budoucnu očekávat růst teploty vzduchu, spojený s časově proměnlivější distribucí srážek a častějším výskytem extrémních klimatických událostí. Kombinovaný efekt výše zmíněných faktorů může na jedné straně způsobit častější, intenzivnější a déletrvající sucha, na druhé straně intenzivní bouřky, doprovázené vysokými srážkovými úhrny, povodněmi a půdní erozí. Klíčovým faktorem pro produktivitu RRD je dostupnost půdní vláhy. S ohledem na očekávanou změnu klimatu v budoucnu, je žádoucí zodpovědět otázky, týkající se produktivity biomasy RRD v situacích, kdy bude půdní vláhy nedostatek.

Hlavním cílem předkládané disertační práce je tedy hodnocení vlivu snížené dostupnosti půdní vláhy na produktivitu RRD a využití vody, na úrovni jedince i porostu. K tomu účelu byl v roce 2011, v rámci produkční plantáže RRD (*Populus nigra* × *Populus Maximowiczii*) na orné půdě v podmínkách Česko-Moravské vysočiny založen třikrát replikovaný manipulační experiment. Tento experiment sestával z páru kontrolní 25 m² a přilehlé 25 m² parcely, osazené konstrukcí se střešními zákryty, jež

odváděly ~70 % podkorunových srážek mimo parcelu. V rámci kontrastních parcel byly monitorovány přírůsty nadzemní biomasy, transpirace a efektivita využití vody. Výpočet transpirace byl založen na sezónním (1. dubna až 30. září) měření transpiračního proudu na kmenech celkem 18 stromů Granierovou metodou disipace tepla. Experimentální 1 ha plantáž byla založena v roce 2002 a poprvé sklizena po 7 letech v roce 2009. Tento experiment zde probíhal od roku 2011 (tj. 3 až 7 rok druhého pěstebního cyklu), přičemž blíže analyzovány jsou vegetační sezony 2012–2015. Design experimentu očekávaným způsobem snížil půdní vlhkost zakrytých parcel u 2 experimentálních bloků, u třetího bloku se to podařilo jen v roce 2014, kdy byly bohaté srážky. Za období 2011–2015 se roční produktivita nadzemní biomasy se pohybovala mezi 5.4–16.2 t ha⁻¹ (v sušině) v závislosti na dostupnosti půdní vláhy u konkrétní parcely. Průměrná roční produktivita během druhého pěstebního cyklu (2009–2015) dosáhla 11.7 a 10.7 t ha⁻¹ u kontrolních a zakrytých parcel, respektive. Nejvyšší výnosy byly zaznamenány v 5. roce (2013). Za 7 let kontrolní parcely vyprodukovaly 81.9 t ha⁻¹ a zakryté parcely 75.0 t ha⁻¹. U dvou ze tří bloků experimentální zakrytí snížilo dostupnost půdní vláhy, což vedlo ke snížení produktivity biomasy o 17.5 % za období 2012–2015. Po dobu trvání experimentu byl pozorován a kvantifikován konkurenční boj jednotlivých stromů o limitované zdroje, který vyústil v diferenciaci stromů na dominantní, které prospívaly a potlačené, které postupně usychaly. Mortalita stromů (na úrovni pařezu) během let 2011–2015 průměrně vzrostla o 1.7 % a 8.5 % u kontrol zakrytých variant, respektive. Spotřeba vody transpirací dosáhla u průměrného stromu, rostoucího v kontrole 3.24 kg den⁻¹ a pro strom v zakryté variantě to bylo 3.08 kg den⁻¹. Přepočteno na transpiraci porostu průměrná transpirace kontrolních variant dosáhla 2.19 mm den⁻¹ a u zakrytých 1.98 mm den⁻¹. Celkový úhrn transpirace v růstových sezonách 2011–2015 dosáhl průměrně 61 % a 55 % referenční evapotranspirace (ET_o) pro kontroly a zakryté plochy, respektive. Vztah mezi produkcí biomasy a vodou spotřebovanou transpirací byl vyjádřen pomocí tzv. efektivity využití vody (WUE), která v kontextu předkládané práce představuje podíl sezónní produkce nadzemní dřevní biomasy a vytranspirované vody. Během vegetačních období 2012–2015 dosáhla WUE 3.17 g kg⁻¹ pro kontroly a 3.00 g kg⁻¹ pro zakrytou variantu. Zároveň zjištěn vztah nepřímé úměry mezi WUE a dostupností půdní vláhy, tzn. plantáž RRD je schopna sníženou dostupnost vody vyvažovat vyšší WUE. Schopnost zvýšit WUE

v reakci na vodní deficit je nezbytným předpokladem pro odolnost proti suchu a také důležitým parametrem pro kritéria šlechtění nových, odolnějších topolových hybridů.

Předkládaná disertační práce sumarizuje vědecké poznatky z oblasti vodního režimu RRD a jeho vztahu k produkci sklíditelné nadzemní biomasy. Tyto výsledky mohou přispět k lepšímu porozumění adaptačním mechanismům plantáží RRD na sušší klimatické podmínky, očekávatelné v blízké budoucnosti, zároveň mohou napomoci při managementu stávajících plantáží a při výběru vhodných lokalit pro pěstování RRD v budoucnu.

1 INTRODUCTION

1.1 Environment of Plants

In the distant geological past, the first plants evolved in environments consisting of water, air and rock (Schulze et al., 2005). Later, soil systems, i.e., the pedosphere, formed with assistance of microorganisms and animals and served as the principal substrate for plants to grow. The environment affects an organism in many ways, at any time. To understand the reactions of a particular organism in a certain situation, individual external influences, so-called environmental factors, are usually considered separately, if at all possible (Schulze et al., 2005). Every environmental factor influences plant growth and development (Wilkinson, 2013). Hydrosphere, atmosphere, pedosphere – all factors influencing plants, or more generally organisms, are called the environment (Breckle, 2002; Larcher, 2003). However, a plant's environment is determined also by all the physical and chemical factors characterizing habitats, and by the influences of other co-occurring organisms, which either favor from or harm plant survival and success. Environment, thus, is the combination of all biotic and abiotic external factors acting upon individual living organisms or a community of organisms in their habitats (Larcher, 2003; Wilkinson, 2013). Biotic environmental factors, resulting from interactions with other organisms, are, for example, infection or mechanical damage by herbivory or trampling, as well as effects of symbiosis and parasitism. Abiotic environmental factors include radiation, temperature, humidity, the supply of water and minerals, and CO₂ (Schulze et al., 2005).

1.1.1 Stress factors

Plants are bound to places. Most plants grow in environments that are, to a certain degree, unfavorable for plant growth (Boyer, 1982). In consequence, they have developed numerous sophisticated adaptations, some of which are unique in the biological world (Boyer, 1982; Osakabe et al., 2012). Roots and stems gather and distribute sparse water and nutrients, surface tissues and stomata conserve water, and leaves intercept solar radiation. Because these features make plants non-mobile, terrestrial plants, unlike animals, could not escape from adverse conditions, and thus should evolve the mechanisms for tolerant toward the adverse conditions (Boyer, 1982; Fitter a Hay, 2001; Osakabe et al., 2012; Popko et al., 2010). Plants almost never find the optimal quantities or intensities of all essential abiotic factors. Thus the

“physiological normal type” is rather the exception and deviation from the rule. It is very important to realize that growth is only one of many reactions of a plant to its environment. Therefore, plants have to be considerably more adaptable to stressful environments and must acquire tolerance to multiple stresses than animals and humans. Plant development and growth are, therefore, very flexible, and capable of responding to environmental influences; for example, plants can add new modules to replace tissues destroyed by frost, wind or toxicity (Fitter and Hay, 2001). Environmental factors can be of abiotic and biotic nature. Biotic environmental factors, resulting from interactions with other organisms, are, for example, infection or mechanical damage by herbivory or trampling, as well as effects of symbiosis or parasitism. Abiotic environmental factors include temperature, humidity, light intensity, the supply of water and minerals, and CO₂; these are the parameters and resources that determine the growth of a plant. Many other influences, which are only rarely beneficial to the plant (wind as distributor of a pollen and seeds), or not at all beneficial or are even damaging (ionizing rays or pollutants), are also classified as abiotic factors. The effect of each abiotic factor depends on its quantity. With optimal quantity or intensity the plant grows “optimally” and thus achieves its potential “physiological normal type”, maximizing its physiologically achievable performance. Most plants require a similar balance of resources—energy, water, and mineral nutrients to maintain optimal growth (Chapin III et al., 1987). Where the environment offers abundant resources, few physical or chemical constraints on growth, and freedom from major disturbance, the dominant species will be those which can grow to the largest size, thereby obtaining the largest share of the resource cake by overshadowing leaf canopies and widely ramifying root systems (Fitter and Hay, 2001). Natural environments, however, differ by at least two orders of magnitude in the availability of these resources. Light intensity varies 100-fold from the canopy to the floor of a rainforest (Björkman, 1981); annual precipitation ranges 500-fold (10–5000 mm yr⁻¹) from deserts to tropical rainforests; and the amount of nitrogen available to plants varies from 0.09 g m² yr⁻¹ in polar desert (Dowding et al., 1981) to 22.8 g m² yr⁻¹ in a rich tropical rainforest (Vitousek, 1984) (in Chapin III et al., 1987). Deviations from the physiological normal type are regarded as reactions to suboptimal or damaging quantities or intensities of environmental factors, i.e. situations for which the term stress is used (Niinemets, 2010; Schulze et al., 2005). Thus, stress and reactions caused by it (stress reactions) can be used as a measure of the strength of the

stress on a scale of intensity, ranging from deficiency to excessive supply. Environmental factors deviating from the optimal intensity or quantity for the plant are called stress factors. If the dosage is inappropriate, stress is caused, as is obvious with the effects of the following factors: light (weak light, strong light), temperature (cold, heat), water (drought, flooding), nutrients (lack of ions, over-fertilization, salt stress), carbon dioxide and oxygen. Usually, an organism is subjected to several stress factors, e.g. lack of water and heat, or a “secondary” stress factor follows the “primary” one: When the plant lacks water and closes its stomata, internal CO₂ deficiency occurs when the plant is illuminated, and as a further consequence oxidative stress ensues. Combination of several stress factors is the normal case and is referred to as multiple stress (Chapin III et al., 1987; Niinemets, 2010; Schulze et al., 2005). While the structural and physiological traits responsible for single factor tolerance are becoming increasingly well understood (Macedo, 2012; Mittler, 2006; Osakabe et al., 2012; Schreiber et al., 2013; Wikberg and Ögren, 2007), the factors responsible for the tolerance to multiple environmental drivers are currently poorly understood (Chapin III et al., 1987; Niinemets, 2010; Wilkinson, 2013). Farmers and breeders have long known that often it is the simultaneous occurrence of several abiotic stresses, rather than a particular stress condition, that is most lethal to crops. Drought and heat stress represent an excellent example of two different abiotic stress conditions that occur in the same field simultaneously (Mittler, 2006). Elucidating plant responses to resource imbalance requires a multidisciplinary approach. The study of resource availability falls in the provinces of community or ecosystem ecology, micrometeorology, and soil science. The metabolic and structural bases of plant responses fall within the realms of physiology, biochemistry, and functional anatomy. Plant physiological ecology borrows heavily from all these disciplines to concentrate on the interface between organism and environment (Chapin III et al., 1987). The physiological processes that produce growth – photosynthesis, respiration, cell division and expansion, activity of growth-regulating hormones, absorption and use of water and nutrients, movement of substances in the plant, and so on – are set by a tree’s genes. But these processes function in a fluctuating environment and are modified by it. It is therefore crucial to understand how temperature, sunlight, day length, water and nutrient availability, relative humidity, atmospheric pollutants, and other environmental variables regulate physiological processes (Dickmann et al., 2002).

1.1.2 Radiation

All life on earth is maintained by the flow of energy that is emitted by the sun and enters the biosphere. Through photosynthesis – the largest-scale synthetic process on earth – which is fundamental to plant metabolism, this radiation energy is fixed in plants in the form of latent chemical energy, from which all links in the food chain derive the energy to carry on vital processes (Breckle, 2002; Larcher, 2003; Nobel, 1991; Schulze et al., 2005). In radiometric units the radiant flux density of solar irradiation (irradiance) perpendicularly incident on the earth's atmosphere — the “solar constant” — is about 1366 W m^{-2} . Atmospheric conditions, such as clouds, permit an average of only 58 % of this sunlight to reach the earth's surface. About 5 % of the photons incident on the earth's atmosphere are in the UV (below 400 nm), 28 % in the visible, and 67 % in the IR (beyond 740 nm). Only about 1.5 % of the radiant energy absorbed by photosynthetic pigments is used to form ATP and NADPH in chloroplasts and ultimately stored by plant cells. In the same photosynthetic cells, in other plant cells, and in animal cells, the carbohydrates formed during photosynthesis can serve as the energy source for mitochondrial respiration, which leads to the generation of ATP by oxidative phosphorylation (Nobel, 1991). Moreover, solar radiation is the largest energy source and is able to change large quantities of liquid water into water vapor (Allen et al., 1998). Thus, radiation represents the primary source of energy for the synthesis of organic material, and by regulation the heat and water balance of the earth it provides the necessary energy for life on earth (Larcher, 2003). Due to differences in the position of the sun, the potential radiation differs at various latitudes and in different seasons (Allen et al., 1998). The radiation angles, dependent on the latitude, also explain the sequence of seasons in different latitudes and the difference between the northern and southern hemispheres (Breckle, 2002). For plants, however, solar radiation functions also as a stimulus for development processes, and occasionally as a stress factor (Larcher, 2003). For poplar as a pioneering tree species the sufficient irradiation is necessary in order to maintain a rapid growth rate (Dickmann et al., 2002).

1.1.3 Temperature

Plants are unable to maintain their cells and tissues at a constant temperature, their metabolism, growth and development are profoundly affected by changes in environmental temperature. The complexity of the thermal environment of plants is matched by the complexity of their responses to temperature. The temperature of a leaf

at given time is determined by a range of factors, such as time of day, month of year, cloudiness, wind speed, position in the canopy, height above surface, canopy characteristics, etc. Plant growth and reproduction can depend on a range of thermal parameters, including: mean, minimum and maximum temperature or the amount of accumulated temperature above a threshold during the whole growing season. Plants responses to temperature can be expressed in terms of three cardinal temperatures: the minimum and maximum temperatures at which the process ceases entirely, and the optimum range of temperature over which the highest rate can be maintained. The cardinal temperatures of higher plant processes vary widely within the range – 10 to 60 °C, and are normally related to the temperature regime in the native range of the species (Fitter a Hay, 2001). For poplar-based short rotation coppice, grown under conditions of central Europe, heat waves rather than freezing temperatures are of higher importance, at it can substantially decrease yields. Late spring frost can cause a some damage to foliage, but it usually does not represent a lethal stress (Verwijst et al., 1996). Heat stress often affects plants simultaneously with other environmental stresses, such as drought (Rouault et al., 2006). Heat stress is often defined as the rise in temperature beyond a threshold level for a period of time sufficient to cause irreversible damage to plant growth and development. In general, a transient elevation in temperature, usually 10–15 °C above ambient, is considered heat shock or heat stress (Wahid et al., 2007). However, heat stress is a complex function of intensity (temperature in degrees), duration, and rate of increase in temperature. The extent to which it occurs in specific climatic zones depends on the probability and period of high temperatures occurring during the day and/or the night. Heat tolerance is generally defined as the ability of the plant to grow and produce economic yield under high temperatures. However, while some researchers believe that night temperatures are major limiting factors others have argued that day and night temperatures do not affect the plant independently and that the diurnal mean temperature is a better predictor of plant response to high temperature with day temperature having a secondary role (Willits a Peet, 1998).

1.1.4 Wind

Plants are living, synthesizing, growing, respiring, and decaying in a fluid that is generally in a state of motion. This air in motion exchanges momentum, heat, gases, and particulates between canopy elements and/or between the canopy layer and the atmosphere. Physical, biological, and chemical processes that control the rate of

turbulent transfer are intimately coupled and atmospheric environmental conditions influence biochemical sources and sinks of H₂O, CO₂, O₂, O₃, terpenes, and isoprenes. In turn, the presence of vegetation in the flow modifies environmental conditions through its influence on turbulence production. Vegetation–atmosphere transfer of momentum and scalar entities (heat, H₂O, CO₂, O₃ and atmospheric pollutants) influences environmental conditions and processes, including the energy and water balance of the surface, vegetation temperatures, the deposition and reentrainment of dust and other particles, and wind damage to forests and crops. Investigations of the deposition of (Wilkinson, 2013). In this way wind can influence plant growth, reproduction, and distribution and in some cases can be lethal (Harrington a DeBell, 1996; Nobel, 1991). Forest damage associated with high velocity winds is an important risk factor in production forestry but is often dismissed as being unpredictable and beyond management control (Harrington a DeBell, 1996).

1.1.5 Water and drought

Drought stress is one of the most important limitations for biomass production and development of any plant (Boyer, 1982; Fitter a Hay, 2001; Popko et al., 2010). Physiological responses of trees to low soil water potential vary from concomitantly lower leaf water potential (anisohydric response) to maintenance of leaf water potential above a threshold (isohydric response) with various strategies in between. Many tree species shed leaves during a strong drought, reducing transpiration and photosynthesis, and adjust partitioning to roots and storage. Drought also ‘weakens’ trees and makes them more susceptible to insect attacks and pathogens (McDowell et al. 2008). In fact, a variety of physiological processes respond at different plant water potentials, so that the severity of the drought will influence the physiological response (Ryan, 2011). Because of the complexity of plant – water relations, there is no single index of water supply by the environment, which can be used to quantify the degree of water deficit stress (or waters stress) to which a plant is subjected. In the absence of such index, it is the convention to quantify water stress in terms of the extent to which tissue water content has fallen below that at full turgor (i.e. below the optimum water content for growth and function). Since the photosynthetic uptake of CO₂ *via* open stomata is inevitably associated with water loss to the atmosphere and some loss of turgor, nearly all plants are exposed to some degree of water stress throughout their lives during the daily period of illumination. Coping with water stress is a routine aspect of plant life,

not simply a feature of species adapted to dry habitats. The primary effect of dehydration on plants is loss of turgor. Under moderate stress there is further reduction in turgor, leading to narrowing of stomatal aperture and progressive reduction of photosynthetic activity. Increased respiration also play a part in stomatal closure owing to an increase in CO₂ concentration within the leaf air space. With the onset of severe stress, photosynthetic exchange of CO₂ ceases followed by high rates of respiration. Xylem begins to show symptoms of xylem cavitation and reduced xylem conductance, accompanied by changes in the synthesis and transport of growth substances. In summary, exposure of plants to even mild water stress can affect growth, and disturb metabolic processes. Depending on their severity, such effects can reduce the ability of the plant to survive and reproduce (Fitter a Hay, 2001). In case of breeding short rotation coppice the drought resistance can compromise the productivity. For instance, increased stomatal control of transpiration increases drought resistance and water-use efficiency (Farquhar et al., 1989), but concomitantly limits maximum photosynthetic rate, and thus growth (Wikberg a Ögren, 2007). Trade-offs may also exist among traits affecting the hydraulic pathways that supply water to the leaves. For instance, increased allocation of growth resources to xylem conduit and fiber wall thickening will increase resistance to xylem cavitation and, hence, increase a plant's resistance to drought, but it will divert growth resources from leaf growth and thus reduce relative growth rate (Hacke a Sperry, 2001; Wikberg a Ögren, 2007). Similarly, increasing the relative allocation of growth resources to roots will increase drought resistance, but reduce harvestable biomass (Sperry et al., 1994). Larchevêque et al. (2011) droughted two different hybrid poplar saplings (each with *Populus balsamifera* as a parent) and compared their response with that of saplings of *P. balsamifera*. The study found that the three poplar clones had three different responses to drought. While all were anisohydric, they showed varying degrees of regulation of leaf water potential, differences in shedding leaves, root growth and stem growth, and differences in water use efficiency. These variable responses among closely related species suggest that both predicting drought response and selecting for drought tolerance on the basis of any simpler metric besides actual growth under drought will be difficult.

1.2 Climate change

At present scientific community no longer debates, whether global climate change exists or not, but attempts to examine the expected outcomes of this process. Each of the last three decades has been successively warmer at the Earth's surface than any preceding decade since 1850. In the Northern Hemisphere, 1983–2012 was likely the warmest 30-year period of the last 1400 years. IPCC report (2014) made a statement, that human influence has been the dominant cause of the observed warming since the mid-20th century. The atmospheric concentrations of carbon dioxide, methane, and nitrous oxide have increased to levels unprecedented in at least the last 800 000 years. Carbon dioxide concentrations have increased by 40% since pre-industrial times, primarily from fossil fuel emissions and secondarily from net land use change emissions and will dominate future scenarios of global environmental change. The ocean has absorbed about 30% of the emitted anthropogenic carbon dioxide, causing ocean acidification. Humans are now the main cause of changes of Earth's atmospheric composition and thus the drive for future climate change (Hansen et al., 2013). This is evident from the increasing greenhouse gas concentrations in the atmosphere, positive radiative forcing, observed warming, and understanding of the climate system.

Trees provide a natural mitigation strategy by capturing and storing CO₂ in their biomass and in soil, while in turn releasing oxygen back to atmosphere. Establishing fast-growing poplar windbreaks, shelterbelts and short rotation plantation thereby hold promise as a viable carbon sequestration strategy. However, emissions of greenhouse gasses will affect the future health and productivity of poplars, as poplars are very sensitive to climate change episodes (Dickmann et al., 2002).

Elevated CO₂ increases photosynthesis and subsequent growth rates and leaf area in poplars, thereby increasing whole-tree photosynthesis and subsequent growth of the trees. However, when poplars are exposed to elevated CO₂ and O₃ simultaneously, as they may be in future climates, the positive effect of CO₂ on growth is offset and often negated by O₃. In addition, the incidence and severity of stresses caused by poplar insects, diseases, and drought also may increase under elevated interacting CO₂ and O₃. Certain poplar clones are more tolerant to air pollutants than others, so selection for tolerance to atmospheric pollutants or interacting stresses may be very important as new generation clones are developed and tested by genetic improvement programs (Dickmann et al., 2002). The counterbalancing effects of increasing water deficit and

rising CO₂ concentration are the main factors expected to modify forest production. The effects of climate change are predicted to be the most severe in short rotation forestry such as poplar plantations, and the severity of the effects is expected to decrease for less intensively managed forests with longer rotations and low productivities (Loustau et al., 2005). Thus, in the future the overall effect of interacting stresses on tree growth may result in lower growth rates for many hybrid poplar clones (Isebrands et al., 2000). Fortunately, the large genetic diversity of poplars will likely allow us to continue our environmental use of poplar well into the future (Dickmann et al., 2002).

1.3 Drought assessment

Drought is a recurring phenomenon that has plagued civilization throughout history. It affects natural habitats, ecosystems, and many economic and social sectors, from the foundation of civilization—agriculture—to transportation, urban water supply, and the modern complex industries (Heim Jr, 2002). Droughts are, by nature, regional phenomena (Alley, 1984). The wide variety of sectors affected by drought, its diverse geographical and temporal distribution, and the demand placed on water supply by human-use systems make it difficult to develop a single definition of drought (Heim Jr, 2002). Drought may be defined as a negative deviation of water balance from the climatological norm over a given area. This implies that drought is a result of deficiency in precipitation over an extended period of time, whereas other meteorological elements (such as increased air temperature, global radiation and wind, as well as decreased air humidity) drive up water demand through increased evapotranspiration (Allen et al., 1998). As the climate change is underway, the frequency, intensity and duration of heat waves increase over Europe. Recently, in the Czech Republic, increased global radiation and air temperature together with decreased relative humidity led to increases in the reference evapotranspiration in all months of the growing season. Several factors will promote more frequent droughts: earlier snowmelt, higher temperatures and higher variability in precipitation. For ecosystems where the water cycle is dominated by snowmelt, warmer temperatures bring earlier melt and longer, drier snow-free periods (Westerling et al., 2006). Greater variability in precipitation has two implications for plant water balance: longer periods without water, and less captured in the soil in the more intense storms (Ryan, 2011). Moreover, the areas with the most pronounced drying trend are located in the most productive

agricultural areas. This is going to be a serious issue for agricultural production to deal with in following years (Brázdil et al., 2007; Trnka et al., 2014). First step in mitigating drought impacts is the definition of drought-threatened areas, by applying appropriate drought assessment indices.

1.3.1 Palmer drought severity index

The World Meteorological Organization (WMO) defines a drought index as “an index which is related to some of the cumulative effects of a prolonged and abnormal moisture deficiency” (Heim Jr, 2002). It is possible to define drought in terms of meteorological, hydrological, agricultural, and socio-economic conditions (Lloyd-Hughes a Saunders, 2002). For this reason, several indicators exist that attempt to encapsulate drought severity on a regional basis. Perhaps the best known is the Palmer Drought Severity Index (PDSI) (Alley, 1984; Palmer, 1965; Sheffield et al., 2012). The method takes into account precipitation, evapotranspiration and soil moisture conditions (Alley, 1984). It applies a two-layer bucket-type model for soil moisture computations with three assumptions related to soil profile characteristics:

(i) the water-holding capacity of the surface layer is set at a maximum of 25 mm, (ii) the water-holding capacity of the underlying layer has a maximum value that depends on soil type, (iii) water transfer into or out of the lower layer only occurs when the surface layer is full or empty. The PDSI itself can be described as an accumulative departure relative to local mean conditions in atmospheric moisture supply and demand at the surface (Palmer, 1965) and it is considered a good representation of episodes of prolonged drought. Moreover, the PDSI calculation includes an intermediate term known as the Palmer moisture anomaly index (or Z-index), which is a measure of surface moisture anomaly for a given month without the consideration of the antecedent conditions so characteristic of PDSI. It is basically the moisture departure, adjusted by a weighting factor known as the climatic characteristic. The Z-index can be used to track drought events on a monthly basis as it responds relatively quickly to changes in soil moisture. The capacity of the Z-index to rank the dryness or wetness of individual months makes it especially useful as one of the indicators of short spells of drought (Brázdil et al., 2014; Palmer, 1965). Thus, the Palmer (1965) indices, computed on a monthly timescale show short-term (Z Index) and cumulative long-term (PDSI) drought and wet spell conditions (Brázdil et al., 2014; Heim Jr, 2002; Palmer, 1965).

1.3.2 Assessment of meteorological drought in studied area using Palmer drought indices

For purposes of this thesis the Palmer drought severity index (PDSI) was used to document the occurrence of drought episodes in studied area and to illustrate its severity in recent years. Firstly, the PDSI was calculated based on long-term meteorological data (1961–2014). In the next step, the Z Index was used for basic trend analysis in selected months over period 1961-2014. The computation of Palmer's indices was performed through following steps: 1) Calculation of monthly values of precipitation, evapotranspiration (Thornthwaite, 1948), soil moisture loss and recharge, and runoff. Potential and actual values were computed for the last four. Means of the potential and actual values for these parameters were computed over a calibration period 1961–2014. 2) Summary the results to obtain coefficients (of evapotranspiration, recharge, runoff, and loss) that are dependent on the climate of the location being analyzed. These coefficients were computed by dividing the mean actual quantity by the mean potential quantity. 3) Re-analyzing the series using the derived coefficients to determine the amount of moisture required for “normal” weather during each month. 4) Computation of the precipitation departure for each month, then conversion the departures to indices of moisture anomaly (Z Index). This moisture anomaly index has come to be known as the Palmer Z Index and reflects the departure of the weather of a particular month from the average moisture climate for that month, regardless of what has occurred in prior or subsequent months (Palmer, 1965). 5) Analysis of the index series in order to determine the beginning, ending, and severity of the drought periods. In Palmer's computations, the drought severity for a month depends on the moisture anomaly for that month and on the drought severity for the previous and subsequent months (Heim Jr, 2002; Lloyd-Hughes a Saunders, 2002). The trend analysis of the long term course of PDSI and Z Index was performed using Statistica 10 software.

The Fig. 1 show comparison of two monthly Palmer drought indices – the PDSI and the Z Index. The magnitude of PDSI range between -4.65 to 5.72. The longest period of drought according PDSI index lasted 4 years since March 1968 until March 1972, with most severe drought during winter 1969–1970 with PDSI index as low as -4.65 in February 1970 and average PDSI value -2.5. This drought period was interrupted by slightly positive values during growing season 1972, but then drought took over until

May 1974. The second longest drought period persisted since April 1988 until October 1991. As the most critical of this period seem to be the entire year 1990 with first 5 months of year 1991, during which period the PDSI remained below -3, which represents “severe drought” (Alley, 1984; Palmer, 1965). During winter 1991–1992 the PDSI was slightly positive, but it became negative soon in April 1992 and remained so until July 1994 with average PDSI -2. The third largest drought started in February 2011 and continues through the end 2014 (end of database), which is almost 4 years. Average PDSI for this period is -2.2.

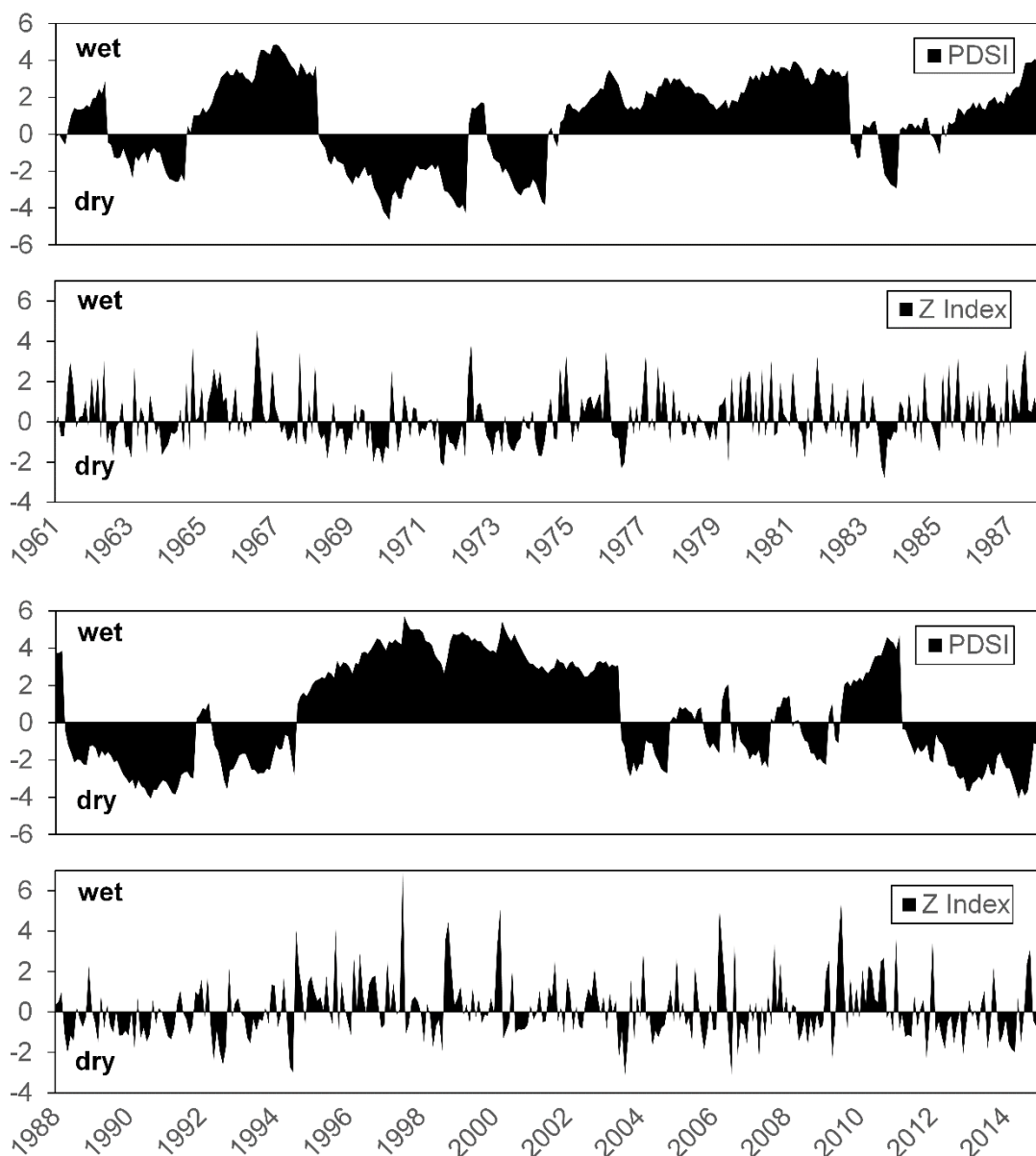


Figure 1: Comparison of two monthly Palmer indices (the PDSI and the Z Index) over period 1961-2014 at Domanínek locality.

Apart from drought, there were also distinctly wet periods, e.g. August 1964 to February 1968, with average PDSI 3.1. The longest and most intense wet period prevailed since August 1992 until May 2003, with average PDSI 3.58 and the highest PDSI value of the whole period 1961–2014, 5.72 in July 1997. Also the Z index reaches its maximum value 6.91 for July 1997. This month is remarkable, since eastern half of Czech Republic has been stricken by extraordinary rainfall (207.8 mm for Domanínek), followed by catastrophic floods (Brázdil et al., 2007). The second longest wet period lasted almost 8 years since October 1974 until August 1982, with average PDSI 2.82. The Z index ranged between -3.15 to 6.91 and exhibited high inter-annual variability, compared to PDSI, as this index characterizes each month separately from other months. If we rank 10 months with lowest Z index (< -2.28) within period 1961–2014, 8 out of 10 driest months happened to be in recent 3 decades and the top three driest months (Z index < -2.98) in last 2 decades, namely July 1994, August 2003 and July 2006.

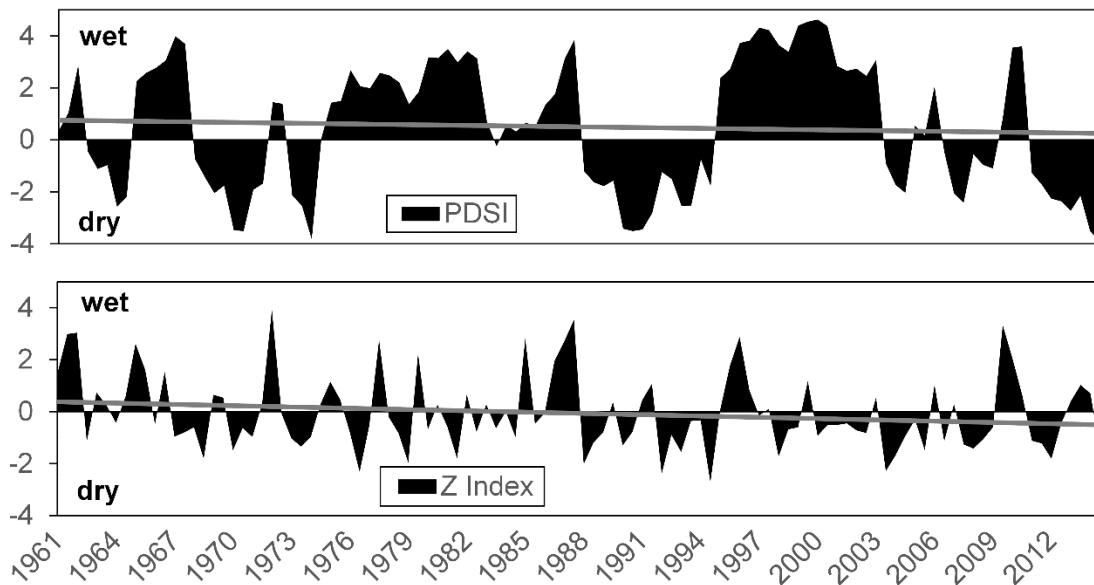


Figure 2: Comparison of PDSI and Z Index in months May and June over period 1961–2014 at Domanínek locality with marked trend lines.

PDSI and Z Index (1961–2014) values for May and June are shown in Fig. 2. There can be seen decreasing trend in both indices (increasing dryness), which is more pronounced in case of Z Index. May and June represent the most sensitive period in terms of agricultural crop vegetative season (Hlavinka et al., 2009). This also includes

short rotation coppice, where most of the stem biomass growth occurs during period May–July.

Table 1: *Trend analysis of Z Index in particular months during period 1961–2014.*

Z Index	April	May	June	July	April- May	March- August	April- July	May- July	May- June
R^2	0.09	0.19	0.17	0.01	0.08	0.10	0.16	0.15	0.23
p value	0.52	0.18	0.21	0.93	0.59	0.46	0.24	0.29	0.09

Tab. 1 shows statistical trend analysis of Z Index in particular month/months of growing seasons 1961–2014. The most pronounced drying trend was found for period May–June, however the statistical analysis did not prove its significance ($p = 0.09$). This result is in accordance with Brázdil et al. (2014), who found clearly negative and statistically significant trends for PDSI in months March–May and June–August, for period 1806–2012 in Czech Republic. This suggests increasing drought risk in the most sensitive part of growing season for agricultural crops.

1.4 Short rotation coppice

The term short rotation coppice (SRC) is generally used for any high-yielding woody species managed in a coppice system usually grown mainly for energy use on arable land. The practice of growing trees on short-rotations to produce woody biomass for the pulp, board and energy industries is known by a variety of names, including short-rotation forestry (SRF), energy forestry in Sweden, short-rotation intensive culture (SRIC) in North America, and short-rotation coppice (SRC) in the UK (Benetka et al., 2002; Djomo et al., 2011; Mitchell et al., 1999). The wood of poplar is very versatile and widely used by the forest products industry. It is light in weight, soft, light in color (except for a dark-colored heartwood or wet wood core), straight-grained, and, because it is diffuse porous, uniform in texture. The wood is used for pulp and paper, veneer, composition boards (especially oriented-strand board, also known as OSB), lumber, and last but not least the energy production (Dickmann et al., 2002). The first industrial poplar plantations were established in Italy at the beginning of the 1900s, producing wood for mechanical pulp and plywood. The trees generally used in the plantations were fast-growing natural hybrids of native and North American species that had been introduced to Europe toward the end of the eighteenth century, usually hybrids of

European black poplar and North American eastern cottonwood (*Populus nigra* L. × *Populus deltoides*) (Fischer et al., 2013b; Hall, 1991; Karacic, 2005; Kauter et al., 2003). Short-rotation forestry has been investigated since the mid-1960s with research focused on growing willows in Sweden (Sirén et al., 1987) and silage sycamore in North America (Steinbeck, 1981) to produce fiber for the paper and pulp industry. In the 1970s, following the oil crises, the emphasis switched to producing woody biomass for energy using fast growing broadleaved trees, such as poplars and willows, grown at close spacing (up to 20 000 plants ha⁻¹) and under intensive management systems more akin to agricultural practice than forestry (Hansen, 1991). Short rotation forestry, particularly coppice (SRC), is now seen in Europe as a means to produce non-food crop on agricultural land which has to be taken out of food production and, hence, a means to provide a future livelihood for farmers. Species being considered for short-rotation forestry include willows in northern and poplars in Western Europe, *Robinia* in the Mediterranean region and *Eucalyptus* in the Iberian Peninsula and part of southern France. Field trials involving these species have been conducted to determine appropriate management systems and to provide reliable data on yield and cost. Ideally, SRC should be established on well-drained, fertile soil, on a site which is flat and free from stones. Both, willow and poplar perform well when the soil is moist throughout the growing season. Willow and poplar have been shown to grow best in mildly acidic soils with a pH of between 6.0 and 7.0. With any commercial planting of trees the most suitable genus, species and provenance or clone should be selected for any given combination of site and climate conditions. Good plantation design should strike a balance between maximizing the benefits of SRC in terms of productivity and efficiency of operations whilst minimizing the detrimental effects on the landscape and the environment. (Mitchell et al., 1999). Field design must attempt to maximize the efficiency of all mechanized operations; long straight rows would be the optimal design, but are unlikely to be acceptable from a landscape point of view. Twin row planting patterns of 75 cm within twin rows, and 150 cm between pairs of rows, and are now accepted as being most efficient spacing to accommodate machinery and allow two rows to be harvested simultaneously. Plant spacing within the rows can be varied to adjust the plant density but is generally around 90 cm (~10 000 plants ha⁻¹). Rotation age is determined by initial plant density and growth rate. In general, planting rates of between 5000 and 20 000 plants ha⁻¹ are used for willow and poplar crops with

corresponding rotations of 3 to 5 years. High initial plant density will facilitate rapid crop establishment, reducing the need for early weed control and may also result in higher yields in the first rotation (Ledin a Willebrand, 1995). Harvesting of SRC crops represents a significant cost in the overall supply chain (up to 70 % (Mitchell et al., 1995b) and, therefore, less frequent harvesting reduces the unit cost of wood production. In addition, repeated harvest can lead to soil damage and plant stress, eventually resulting in the loss of plant vigor and reduced yield; less frequent harvesting may extend the life of a plantation (Sennerby-Forsse, 1997).

1.4.1 Short rotation coppice in the Czech Republic

By the end of year 2012 in the Czech Republic there are 4.22 million ha of agricultural land out of which arable land occupies approximately 70.86 % (~ 2.99 mil ha) (Czech Statistical Office, 2014). Half of the agricultural land is found in less-fortunate areas (LFAs) that are less suitable for production, but may be used for energy crop production (Havlíčková a Suchý, 2010). The area of SRC plantations in Czech Republic registered by Ministry of Agriculture of the Czech Republic increased from 262 ha in 2009, 373 ha in 2010, 772 ha in 2011 to 2088.66 ha (May 30th 2014) (Ministry of Agriculture of the Czech Republic, 2014, pers. commun.). This shows increasing trend of establishing new SRC plantations, but still the total share of SRC on arable land in the Czech Republic is tiny 0.7 %. There is a general agreement that biomass production is the most promising source of renewable energy in Czech Republic (Lewandowski et al., 2006) and if biomass is to become a major fuel then energy cropping would have to become a significant land use category, but there is no reason why this should be at the expense of food production or other existing land uses (Hall a Scrase, 1998).

1.4.2 Poplar

The *Populus* genus comprises a singular group of trees. Poplars are all deciduous or (rarely) semi-evergreen forest trees with a wide distribution in the Northern Hemisphere, from the tropics to the northern latitudinal limits of tree growth. Stem form is characteristically tall and straight (excurrent), but even within a species stems of individuals or clones can be multiply branched (deliquescent) or twisted and convoluted (Dickmann et al., 2002). Poplars are short-lived compared to other trees such as white pine, oaks, or Douglas fir, in large measure because they are host to many diseases and insect pests. Nonetheless, the fast growth rate of poplars often enables them to reach

large size. Especially hybrid poplars are often regarded as “junk trees” because of their short life span, susceptibility to breakage, and predisposition to diseases and insect damage. Poplar trees may produce few coarse branches, or a myriad of fine branches and twigs. Large branches tend to be brittle and are easily broken off by strong winds, wet snow, or ice. In many species, small branches are abscised in a process not dissimilar to autumn leaf abscission, a trait unique to poplars. Poplar bark, which can be creamy white, various shades of gray, olive green, orange–brown, or bronze in color, often remains smooth for many years, especially in the aspens. Lenticels are prominent on the young bark. On older trees, the lower bark breaks up into coarse, corky ridges. In cottonwoods, these ridges may extend well up into the crown. Poplars are major invaders of disturbed sites, but the ecological habitats occupied by the various taxa in the genus break rather cleanly into two categories. Many poplar species typically grow in riparian or wet habitats, ranging from the far northern boreal latitudes to the tropics. Another distinctive feature of the genus *Populus* is its predisposition to form clones by vegetative propagation. (Dickmann et al., 2002). Vegetative propagation of clones enables many plant species to successfully compete and reproduce in the ecological habitats they occupy. Cloning also can be a very effective strategy for invading new habitats. Most important for silvicultural and horticultural applications is the establishment of clonal poplar plants with hardwood stem cuttings. This strictly anthropogenic form of vegetative reproduction employs 20 to 30 cm long (sometimes shorter or longer) sections of dormant, 1 year old woody shoots as planting stock. Amazingly, if these “sticks” are planted in the spring they will quickly produce roots from existing primordia in the inner bark and new shoots from the buds. The resultant clonal plants often grow several meters tall in the first growing season. This trait alone has allowed the widespread and successful planting of poplars in plantations (Dickmann et al., 2002). Root system of *Populus* taxon tree can achieve maximum vertical extent 1.3–3.6 m depth and 1.5–30.5 m for horizontal extent (Pallardy, 2010).

Poplar is a hardy tree species which can withstand a single moderate defoliation by insects and pathogens without major growth losses, but repeated defoliations over several years can have devastating impacts. Defoliation by *Melampsora* leaf rust, which begins in midsummer, can be especially troublesome in high-yield plantations. Volume growth losses of 50–60 % in rust-susceptible clones have been recorded (Widin a Schipper, 1981), and tree death can occur after repeated defoliations. Atmospheric

pollutants also can substantially alter the carbon physiology of poplar trees. Elevated tropospheric ozone (O₃) causes a reduction in the photosynthetic rates of mature leaves of poplar clones and causes leaves in the lower canopy to prematurely senesce and die. Thus, overall whole photosynthesis for the season is decreased. Moreover, this premature defoliation decreases normal carbon allocation from the lower leaves to the basal portions of the stem and to the roots so that seasonal diameter and root growth of trees decreases (Dickmann et al., 2002).

1.4.2.1 Hybrid poplar clone Populus nigra L. × Populus maximowiczii Henry

The male Asian balsam poplar, *Populus maximowiczii* has its natural habitats in Korea which is frequently associated with both broad-leaved species and conifers. The female black poplar, *Populus nigra*, distributed in Europe, Asia, and North Africa, was introduced to Korea in 1958. Black poplar is an aggressive species that seeds into wastelands, riverbanks, and other exposed sites. It sprouts vigorously from stumps and, to some extent, suckers from roots. Propagation from stem cuttings also is very easy. At maturity, black poplar may reach heights of 40 m and diameters of nearly 2 m. Morphologically, *Populus nigra* has slender and round shoots with small leaves. The female tree typically shows short catkins with round, crowned capsules. These species were crossed to create a new clone, Rochester (*Populus. maximowiczii* × *Populus nigra plantierensis*). From the provenance test, the hybrid poplar (*Populus nigra* × *Populus maximowiczii*) is characterized by its fast growth rate, high resistance potential to cold, disease, and acidic soil conditions as well as its suitability for a wide variety for forest lands. Currently, named as “NM6” represents, the most common commercial clone in the North Central U.S. and, named as J-105 or Max 5, is widely planted in the Central Europe.

2 AIMS

As outlined in previous chapters, short rotation coppice is low-demanding, sturdy crop, which thrive at fields, where other agricultural crops fail to deliver economically and ecologically viable production. Nevertheless, the major environmental factor, limiting growth and development of SRC is soil water availability. Climate in the near future is expected to bring increased temperatures, sparse precipitation, thus higher risk of drought occurrence.

Therefore, the main purpose of this thesis is to evaluate responses of an operational short rotation coppice, grown under climatic conditions of Bohemian-Moravian highlands, to decreased soil water availability. The decrease of soil water availability is artificially induced by establishing rain-throughfall exclusion experiment, which reduced the throughfall precipitation water income by 70 %, compared to control treatment. Two main questions are addressed in the first and second chapter:

- Chapter I. What is the actual productivity of harvestable biomass under current climatic conditions, and how the productivity may be affected by decreased precipitation water income?

- Chapter II. What is the actual tree- and stand-water use, how it may change under decreased precipitation water income and what are the minimum water requirements to sustain economically viable productivity?

3 MATERIALS AND METHODS

3.1 Locality

All measurements and analyzes within this study were carried out from June 2011 until October 2015 at research field locality Domanínek (Czech Republic, 49°521'N; 16°235'E, in altitude 578 m a. s. l.), near the town of Bystřice nad Pernštejnem. For purposes of this research infrastructure of experimental station Domanínek operated by Global Change Research Institute CAS was extensively used.

The site is located in the eastern part of Bohemian-Moravian Highlands, which can be described as a hilly, rain-fed area, drained by Svratka River. Upper hilly parts are mostly afforested by spruce forest, middle and lower parts are maintained as an agricultural land, which is considered as rather marginal area in terms of productivity. Soil is characterized by relatively shallow (0.3–0.5 m) luvisc cambisol influenced by gleyic processes and with stones in the profile. The experimental site served in history as an arable land, mostly planted with potatoes and cereals. Nowadays, some parts are transformed into permanent grassland and approximately 6 ha are managed as high density short rotation coppice plantations. Concerning agricultural production, the area represents rather marginal area. The location itself is suitable for poplars (Trnka et al., 2016) as indicated by several black poplar trees (*Populus nigra*) more than 100 years old which stood in the vicinity of the plantation.

3.2 Climate conditions

Generally, the climate is cool and wet temperate, typical for this part of Central Europe with mingling continental and maritime influences (Trnka et al., 2008). The mean annual precipitation is 609.3 mm and mean annual temperature 7.2 °C and the mean annual reference evapotranspiration is 650 mm, based on long term mean (1981–2010) of climate variables (see Tab. 2) at meteorological station Bystřice nad Pernštejnem (Czech Republic, 49° 32' N, 16° 16' E and altitude 560 m a. s. l.), owned by Czech Hydrometeorological Institute. This station is located less than 1 km from the experimental plantation. Mean length of the growing season (daily mean air temperature above 5 °C) is 217 days from March 30 to November 1 (Trnka et al., 2016).

Table 2: Mean air temperature and mean precipitation at experimental site over selected periods of time.

Mean air temperature (°C)	Jan-Dec	Apr-Oct	May-Jul	Nov-March
1961-1990	6.6	12.0	13.9	-0.9
1971-2000	6.9	12.1	14.1	-0.5
1981-2010	7.2	12.7	14.8	-0.5
2011-2015	7.9	13.1	15.2	0.3
Mean annual precipitation (mm)	Jan-Dec	Apr-Oct	May-Jul	Nov-March
1961-1990	578.1	392.9	210.7	185.2
1971-2000	586.8	393.6	205.5	193.2
1981-2010	612.5	407.8	213.4	204.7
2011-2015	507.1	365.5	179.2	141.6

Table 3: Mean air temperature, precipitation totals, ET_o totals and ET_o/P ratio at the study site over selected periods of time.

Mean air temperature (°C)	Jan-Dec	Apr-Oct	May-Jul	Nov-March
2011	7.4	12.9	14.5	-0.4
2012	7.4	13.1	15.8	-0.6
2013	7.3	12.8	15.2	-0.3
2014	8.7	13.1	15.0	2.5
2015	8.7	13.7	15.8	NA
Mean annual precipitation (mm)	Jan-Dec	Apr-Oct	May-Jul	Nov-March
2011	520.6	408.3	229.4	112.3
2012	510.8	325.4	182.4	185.4
2013	529.2	385.6	196.0	143.6
2014	559.2	417.8	175.8	141.4
2015	415.6	290.5	112.3	125.1
ET_o (mm)	Jan-Dec	Apr-Oct	May-Jul	Nov-March
2011	657.8	580.4	303.3	77.4
2012	687.4	614.0	328.9	73.3
2013	635.3	588.2	314.4	47.0
2014	595.4	518.7	312.4	76.7
2015	665.1	587.0	329.5	NA
ET/P ratio	Jan-Dec	Apr-Oct	May-Jul	Nov-March
2011	1.26	1.42	1.32	0.69
2012	1.35	1.89	1.80	0.40
2013	1.20	1.53	1.60	0.33
2014	1.06	1.24	1.78	0.54
2015	1.60	2.02	2.93	NA

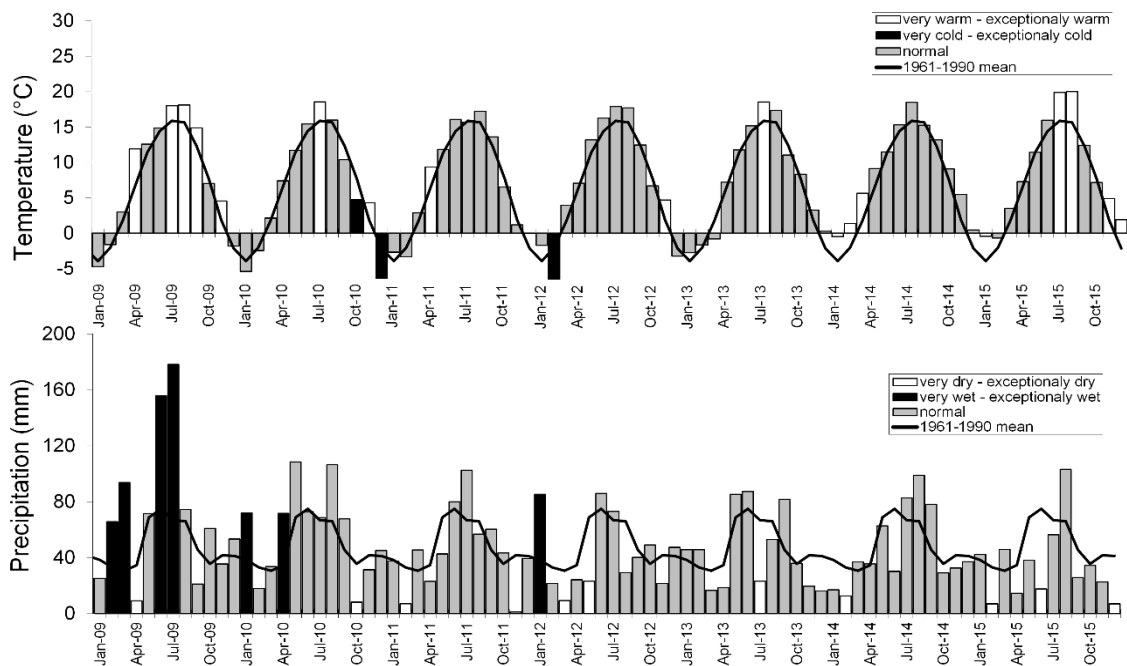


Figure 3: Monthly course of average air temperature and precipitation totals compared to climatological normal 1961–1990.

3.3 Poplar plantation

The first operational short rotation coppice plantation at study site Domanínek (near the town Bystřice nad Pernštejnem, 49°521'N; 16°235'E) with total area of 1 ha was established in April 2002. The plantation was based on hybrid poplar clone J-105 (*P. nigra* L. × *P. maximowiczii* Henry “Maxfünf”). The plantation is situated on an 8° slope, east-facing land, formerly cropped with potato and cereals (Trnka et al., 2008). The plantation has rectangular shape 100 x 100 meters and stretches near the upper part of low ridge having a shallower soil with bedrock outcrops just below the ground and no access to groundwater. Slope decreases from 582 m to 570 m in W–E direction. Hardwood cuttings were planted in a double row design with inter-row distances of 2.6 m and spacing of 0.7 m within rows, accommodating theoretical density of 9 216 trees ha⁻¹. The first rotation cycle length was set at 8 years due to strong weed competition which slowed down the canopy closure and thus the productivity in the first 3 years after planting. In the early spring of 2009 trees from the first rotation were harvested and the plantation was allowed to resprout for the second rotation. Research activities within the frame of this thesis were conducted between years 2011–2015, covering 3rd to 7th year of the 2nd rotation cycle. The second rotation cycle length will last for 8 years as well. The harvest is planned for turn of year 2016 and 2017.

3.4 Experimental design

In mid-June 2011 a throughfall exclusion experiment was established. It consists of two adjacent square-shape plots of 25 m² each - the “throughfall exclusion treatment” (R) with plastic strips intercepting rainfall and ditch exclusion of water runoff and “control treatment” (C) with natural rain water income. The ground area of each plot was well defined as tree and tree row spacing were regular and the plot margins were located just in between two rows of trees. Pair of experimental R + C plots is triple replicated (block 1, 2, 3) within the plantation, at least 25 m from the edges, in order to eliminate influence of edge effect. Each R plot is equipped with a horizontally inclined wooden construction app. 0.5–1 m above ground, which carries narrow roof strips made from transparent plastic. Throughfall rainwater from roofs was diverted at the inclined side of the roof into the drainage pipe and taken away from the plot. Such roof system covers the inter-row space on both sides of the inner double row and can be widened or reduced by adding or removing additional strips. The area of double row was not covered, thus trees could receive some portion of throughfall through this gap, including stem flow. The initial throughfall reduction at R plots was set to 40 %, in order to induce experimental water shortage but not tree dieback. Moreover, after a suggestion given by Dr. John S. King, all R treatments were dug around on June 6th 2012 with trenches of 0.5–0.8 m deep (depending on the bedrock depth). This trenching was performed partly manually and partly using 4 wheel hydraulic digger. After digging was finished, each trench has been insulated with geofoil preventing roots to grow outside the plot and water to flow inside. The real percentage of throughfall reduction at R plots was determined by two gutters, diagonally installed across each treatment at the height of 0.4 m (i.e. below the roof). Comparison of the amounts of water captured in barrels on weekly basis allowed for quantification of actual throughfall displacement rate. Tab. 4 summarizes the partitioning of gross rainfall, ET_o and quantifies throughfall amounts received by C and R treatments in different periods of growing season in years 2011–2015. As there has been observed no apparent decrease in soil moisture at R plots during 2011 and 2012, in mid June 2013 the roof coverage was raised from 40 % up to 70 % (see Fig. 4), which resulted in onset of demanded difference in soil water availability in following growing seasons.

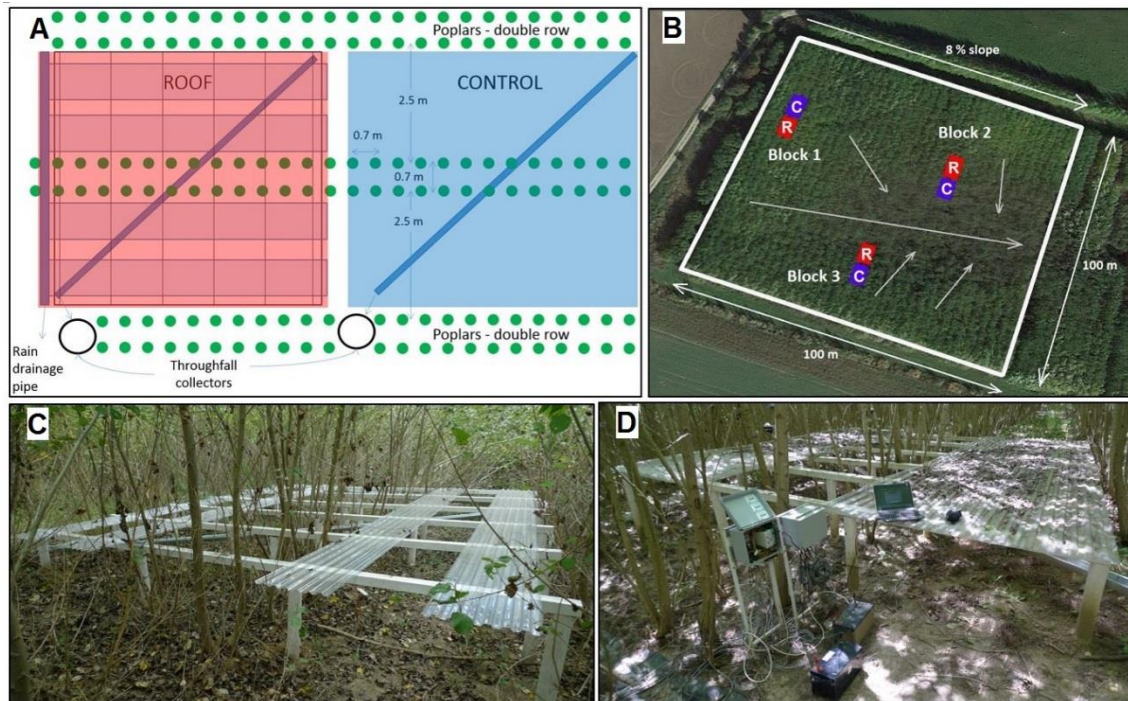


Figure 4: (A) *experimental design layout.* (B) *aerial footage of 1 ha experimental plantation with marked positions of experimental Blocks (replications).* Arrows indicate sloping terrain, along which water leaves the area. (C) *Block 1 with 40 % throughfall exclusion in 2011.* (D) *Block 1 with 70 % throughfall exclusion in 2015.*

3.5 Soil water

3.5.1 Soil moisture

Volumetric soil moisture water content was measured manually using profile probe PR1 (2011–2013) or PR2 (2013–2015) (Delta-T devices) – a system measuring dielectric properties of soil, which are straight depending on soil water wetness. Since June 2011, each experimental plot was equipped by an array of 3 access tubes, which were installed diagonally across each plot, i.e. one tube in lower middle row, one in center double row, one in upper middle row (see Fig. 5). The frequency domain reflectometry (FDR) PR1 profile probe enables to evaluate volumetric content of soil water ($\text{m}^3 \text{m}^{-3}$) in different depths (0.1, 0.2, 0.3 and 0.4 m). It consists of a sealed composite rod (~25 mm in diameter) with electronic sensors (in the form of pairs of stainless steel rings) arranged at fixed intervals along its length. The accuracy of the calibrated probe is $\pm 3\%$ in an access tube and the sampling volume in each of the four measured depths is $\sim 1.5 \text{ dm}^3$. The sensor registers only 120° of the cross section of soil, so three measurements must be taken at each tube, separated from each other by 120°

twist of the sensor rod to get complete information about 360° circumference of the access tube. Measurements with profile probe were taken usually once in two weeks, each year from March till the end of November. Note, that for this study only the data representative for the length of growing season (i.e. April–October) will be evaluated.

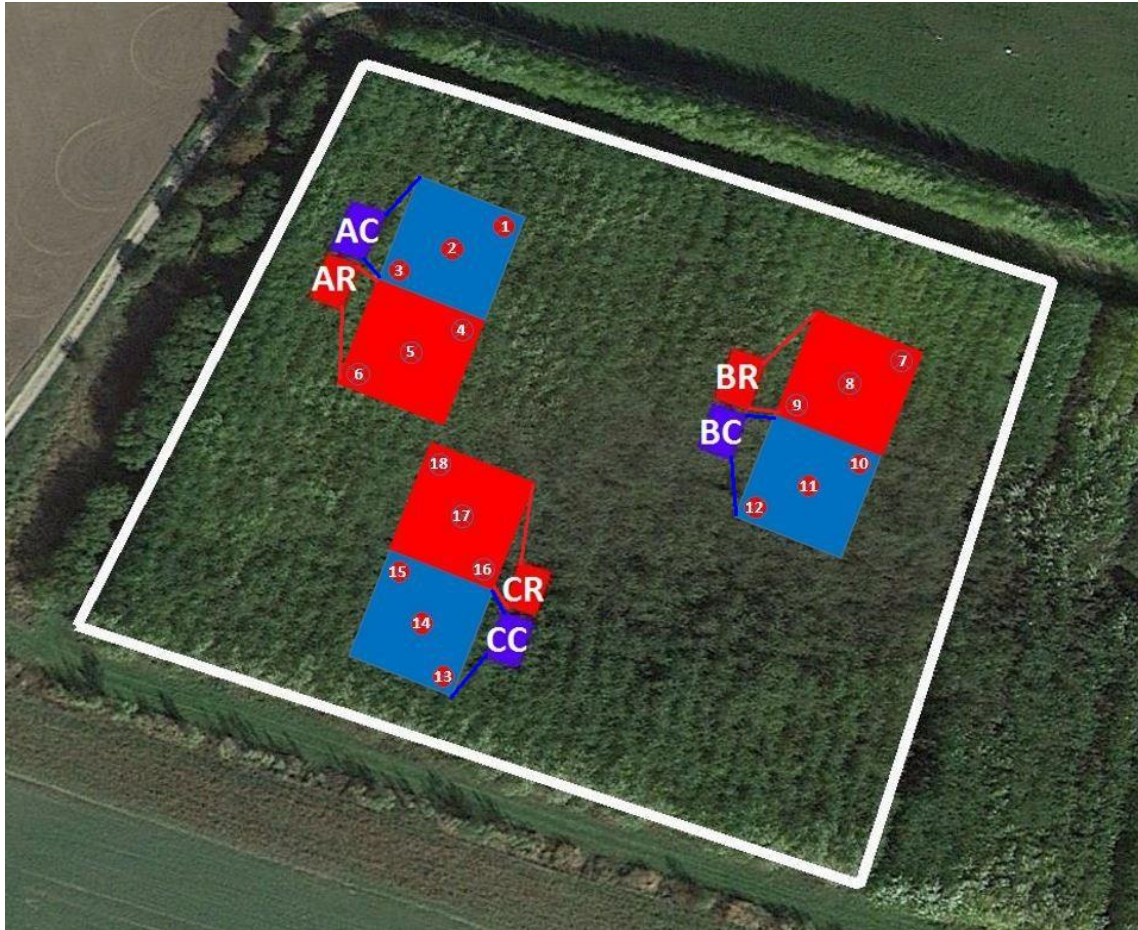


Figure 5: Airborne image of soil moisture monitoring access tubes locations.

3.5.2 Soil water potential

Soil water potential (SWP) profile in depths of 0.1, 0.2, 0.3 and 0.4 m was measured hourly at R treatment of block 1 using gypsum block sensors (Delmhorst GB-1, NJ, US) in order to monitor the intensity of induced drought stress. The gypsum block sensor is capable to measure SWP within the range of -0.3 to -14 bar.

4 CHAPTER I.: ANALYSIS OF DECREASED SOIL WATER AVAILABILITY ON ABOVE-GROUND BIOMASS PRODUCTIVITY

Biomass is nowadays understood as biological mass from which energy can be produced (Karp a Shield, 2008). Given its high-energy content and versatile use, biomass in a form of wood has been used for energy purposes since millennia and all the time is widely preferred source of biomass (Faasch a Patenaude, 2012; Hoogwijk et al., 2005). Wood is one of the most important of nature's raw materials, and it continues to contribute significantly to the standard of living of humankind (Dickmann, 2006). Perlin a Journey (1991) go so far as to say: "Wood, in fact, is the unsung hero of the technological revolution that has brought us from a stone and bone culture to our present age." The world derives a fifth of its energy from renewable resources: 13–14% from biomass. For three quarters of the world's population, who live in developing countries, it is the most important source of energy. In the world's poorest countries up to 90% of all energy is supplied by biomass, whilst the highest rate of biomass use in developed countries is 16–18% in Sweden and Finland respectively. This was stated by Hall (1991) and the situation did not change very much in 25 years ever since. Wood is still the main energy source in a number of countries and regions (e.g. Bhutan 86 %, Nepal 97 %, Asia 16 %, East Sahelian Africa 81 % and Africa 39 %) (Amous, 1999; Bhattarai, 1997; Hoogwijk et al., 2005). The productivity of poplar and willow SRC is largely dependent on the environment in terms of soil characteristics and climatic conditions (Amichev et al., 2010; Broeckx et al., 2013). Biomass yield of poplar short rotation coppice plantations can be severely compromised when water is limiting (Liang et al., 2006). Plantation managers traditionally increase yield by controlling genotype, tree density and nutrient availability. A few intensively managed plantations are irrigated to further increase production (Kim et al., 2008). Nevertheless, there are not many SRC plantations which can be irrigated and remain economically viable. Most of SRC plantations in managed extensively. In such case drought is the major constraint of woody biomass production involving serious economic consequences. One of the climate change consequences is the increasing frequency and duration of heat waves over Europe. Higher temperatures increase evaporation and can intensify droughts when they occur (Brázdil et al., 2014; Liang et al., 2006). Droughts start earlier in the year

and last longer (Beniston et al., 2007; Hansen et al., 2013). King et al. (2013) suggest that widespread bioenergy production will be especially sensitive to future water availability and will potentially compete with other demands for water, a situation that is likely to be exacerbated in many regions because of climate change. In the Czech Republic, increased global radiation and air temperature together with decreased relative humidity led to increases in the reference evapotranspiration in all months of the growing season; this trend is particularly evident in April, May, and August, when more than 80% of the territory shows an increased demand for soil water (Trnka et al., 2014). Fischer et al. (2013) reported the actual evapotranspiration (ET_a) of poplar-based SRWC to be fully comparable to the ET_a of grassy surface under same climatic conditions, reaching about 80 % of reference evapotranspiration (ET_o). In areas where long-term ET_o exceeds precipitation the biomass productivity can be limited, particularly when temporal distribution of precipitation is uneven. This also applies to our study site, where total ET_o was 20 % higher than total rainfall over the period 2010–2015. Given the projected life-span of newly established plantations (about 24–30 years) it is important to understand the response of the SRWC to the expected climate conditions and to lack of water in particular. Thus, the main goal of this chapter is (i) to quantify aboveground biomass productivity of the operational SRWC plantation, (ii) to compare annual productivity and mortality of treatment with partial throughfall exclusion and control treatment with intact rain water income, (iii) to analyze patterns of competitive behavior among trees, which affects the biomass productivity in terms of shift in stand composition and mortality.

4.1 Methods

4.1.1 Above-ground biomass productivity

To estimate the aboveground biomass productivity, the well-known allometric relationships were adopted. The total aboveground dry matter (DM) biomass in kilograms (Y) was related to tree diameter measured at breast height 130 cm (DBH) using the power function: $Y = aDBH^b$, where Y stands for above-ground DM biomass per tree in Kg (including stem and branches), DBH is diameter at breast height (130 cm) and ‘a’ and ‘b’ are regression coefficients, which were tested and fitted every two years, in order to keep the relationship updated and accurate, because allometric relationships were expected to vary with age. The first set of destructive sampling was conducted

during dormant stage before bud burst in early spring 2011. Trees from different parts of plantation were cut at the ground level (~10 cm) and total tree DM biomass including stems and branches was determined after drying at 70 °C until constant weight was reached. Another set of destructive sampling was carried out in year 2013. Last set of destructive sampling was carried out in January 2016, when only 5 dominant trees (DBH 71.8–106.6 mm) were cut and measured in order to improve the function accuracy for bigger trees. There has not been observed any substantial shift in allometric relationship parameterized in 2011 as compared to equation from 2013. Thus datasets from years 2011 (n = 65), 2013 (n = 28) and 2016 (n = 5) were pooled together and allometric equation $Y = 2.96 \cdot 10^{-4} \text{ DBH}^{2.48}$ ($R^2 = 0.99$) was parameterized (see Fig. 1).

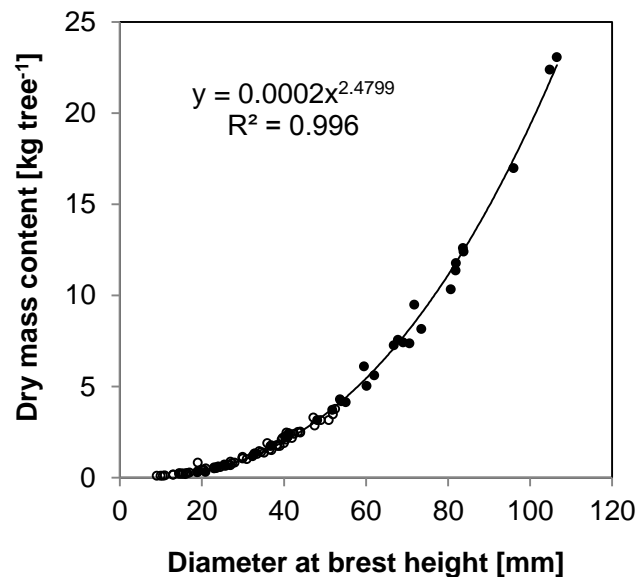


Figure 6: *Final allometric relationship based on datasets from 2011, 2013 and 2016.*

The above-ground biomass productivity (ABP) was determined from annual stand inventory measurements. DBH values of all trees within particular plot were measured manually by digital caliper during dormant stage each winter. Then the abovementioned allometric equation was applied on each tree-related DBH in order to estimate total standing DM biomass per plot in kg. This was in the next step scaled up to the area of one hectare, according number of stools per plot (14–20) and per hectare (9 216). The annual ABP per plot was determined by subtracting the total standing DM biomass of previous year from total standing DM biomass of subsequent year.

4.1.1.1 Mortality

Stool mortality was determined once a year based on stand inventory data. It was calculated as a relative amount of dead or missing stumps in the row.

4.1.1.2 Data analysis

The statistical software R (version 3.2) was used for the most important calculation of the above ground biomass productivity, mortality and for statistical analysis, as well as for plotting of some figures. Pre-processing, less complicated data analysis and simpler graphs were performed in Excel software.

4.1.2 Analysis of dominance

The changes in the stand composition and analysis of competitive behavior (dominance) among trees within the plantation were analyzed using the annual stand inventory datasets. An approach proposed by Binkley (2004) was adopted in order to evaluate whether the above ground biomass productivity might be influenced by competitive relationships among trees. In other words it determines, how many percent of the annual biomass increment at a particular plot was produced by a particular tree. This approach was used to analyze relative contribution of trees of different size to overall annual growth in first (2011) and last year (2015) of the experiment duration. Trees were sorted from smallest to largest for each plot and time period, and the cumulative distribution for stem mass was compared with the cumulative distribution for stem growth. A stand with strong dominance would have notably more than 20 % of the total stand growth contributed by the largest trees that comprise the top 20 % of stem mass.

4.2 Results

4.2.1 Soil moisture patterns and experimental design

In rain fed areas such as our study site Domanínek, the soil moisture storage is refilled solely by precipitation prevailing over transpiration and other loss components of water balance, such as soil evaporation, canopy interception evaporation and runoff. Therefore, the soil moisture is described in linkage to rainfall, throughfall and ET_o amounts as it's driving factors. In Fig. 7 there are depicted 4 boxplots with seasonal courses (April–October) of soil moisture per particular treatment and block. Soil moisture records from three access tubes at particular plot were averaged to obtain a single value representative per profile 0–0.4 m per plot. On Tab. 4 there is an overview of rainfall, ET_o , throughfall and throughfall rain exclusion in given period of growing seasons 2011 – 2015. In 2012 the roofs covered only 40 % of R treatments and seasonal medians of soil moisture are very comparable between neighboring C and R treatments (with exception of block 3). During period May–Jul controls received 160.7 mm from throughfall, whereas R treatments 96.4 mm. This difference might have been mitigated at R treatments by depleting soil moisture reserves from previous year 2011 which was the wettest year of this study (seasonal precipitation of 408.3 mm). Control treatments show higher upper range of soil moisture, due to an unrestricted access to throughfall rainwater. In 2013 the magnitude of soil moisture was wider, meaning that there were wetter as well as drier periods. In mid-June the roof coverage was extended to cover 70 % of the R treatments, so the seasonal median of soil moisture started to develop in favor of C treatments (with exception of block 3). Throughfall in period April–July was sufficient (173.6 mm), while the ET_o was lowest compared to same periods in other years (264.1 mm), what allowed for good productivity this year. Year 2014 was the most humid on seasonal level. The seasonal median of soil moisture at all treatments was well above 20 % as a result of 417.8 mm of precipitation and 488.4 mm of ET_o during period April–October, what represents the highest precipitation amount and lowest ET_o compared to growing seasons 2011–2015. The control treatments received 368.1 mm, whereas the R only 110.4 mm, which made a difference of 257.7 mm. Thus, the treatment effect on the soil moisture was the most pronounced and apparent at all blocks. This is the only year when the soil moisture of C treatment at block 3 exceeded that of R treatment, what was also reflected in annual productivity. Looking at the period May–July – which is the most important period for growth of

stem biomass – the throughfall precipitation amounted only 115.8 mm for C and 30.6 mm for R treatment, whereas the ET_o was as high as 294.1 mm, which resulted in lower biomass yields, compared to what one might have anticipated from seasonal overview.

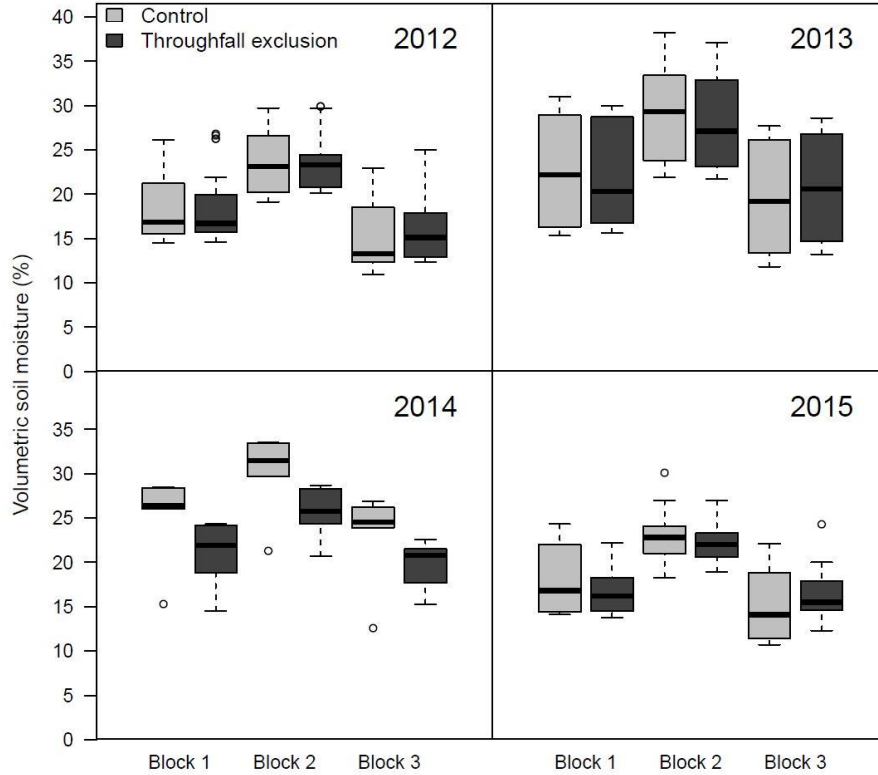


Figure 7: *Boxplot showing seasonal (2012-2015) soil moisture of control and throughfall exclusion treatments of block 1-3 in layer 0-45 cm.*

The driest year was year 2015. Seasonal precipitation was the lowest 290.5 mm, ET_o as high as 560.4 mm. Seasonal throughfall income for C treatment reached 255.9 and 76.8 mm for C and R, respectively. The soil moisture of both treatments was low and the treatment effect was diminished by drought, which affected C treatments with similar severity as R treatments. On a block level, there can be seen, that soil moisture was systematically highest at block 2, then followed block 1 and block 3. Irrespective of drought occurrence in different years nor of the throughfall exclusion treatment, the median soil moisture of block 2 did not decrease below 22 %, which cannot be considered as water-limiting nor even drought-stress conditions for poplar. Block 1 showed medium soil water availability with treatment effect very well developed. Soil

moisture manipulation at block 3 turned up to be quite problematic one. Even with 70 % throughfall exclusion it was not possible to decrease soil moisture below that of C treatments (with one exception in 2014) with all further consequences on productivity and water use.

Table 4: *Overview of rainfall, ET_o , throughfall, throughfall rain exclusion and throughfall rain reduction expressed in mm of water column or percentage in given period of growing seasons 2011 – 2015.*

	2011	2012	2013	2014	2015	
Apr-Oct	Rainfall (mm)	408.3	325.4	375.8	417.8	290.5
	ET_o (mm)	545.4	576.5	520.8	488.4	560.4
	Throughfall at C (mm)	359.7	286.7	331.1	368.1	255.9
	Throughfall at R (mm)	258.0	172.0	173.1	110.4	76.8
	Throughfall reduction (mm)	101.7	114.7	158.0	257.7	179.2
	Throughfall reduction (%)	28.3	40.0	47.7	70.0	70.0
Apr-Aug	Rainfall (mm)	313.6	236.0	258.2	310.4	230.1
	ET_o (mm)	444.4	484.5	445.5	426.8	485.2
	Throughfall at C (mm)	276.3	207.9	227.5	273.5	202.7
	Throughfall at R (mm)	207.9	124.7	142.0	82.0	60.8
	Throughfall reduction (mm)	68.4	83.2	85.5	191.4	141.9
	Throughfall reduction (%)	24.7	40.0	37.6	70.0	70.0
May-Jul	Rainfall (mm)	229.4	182.4	173.6	115.8	112.3
	ET_o (mm)	284.5	309.3	264.1	294.1	313.0
	Throughfall at C (mm)	202.1	160.7	152.9	102.0	98.9
	Throughfall at R (mm)	155.3	96.4	75.1	30.6	29.7
	Throughfall reduction (mm)	46.8	64.3	77.8	71.4	69.3
	Throughfall reduction (%)	23.2	40.0	50.9	70.0	70.0

On Fig. 8 there is depicted seasonal course of soil water potential (SWP) at R treatment of block 1, illustrating potential drought stress. It illustrates the subsequent effect of throughfall exclusion on soil water availability in years 2011–2015. Note, that SWP is in fact a negative value, therefore, numbers on y axis represent negative values of SWP. In 2011 the soil water availability was good. The rise of SWP can be seen at the end of growing season, due to installation of throughfall exclusion roofs. In 2012 the SWP increased earlier and induced water shortage in whole layer 0–0.4 m as a result of trenching. In 2013, the spring water scarcity was partly mitigated by sufficient precipitation during period April–June (191 mm) and low ET_o (231 mm). In June 2013

the roof coverage was increased to 70 %, which increased SWP for following years. In 2014 the drought stress begins early, but in July was eliminated by 71 mm rainfall. In 2015 the SWP showed similar course as in 2014. Drought stress was present in deeper layers until mid-August, when soil water was replenished by 82 mm in one day. Nevertheless, the productivity at R treatment was compromised as a result of decreased soil water availability in June–July – months of growing season important for stem growth. Note, that SWP profile was not monitored at C treatment, in order to the spare financial budget.

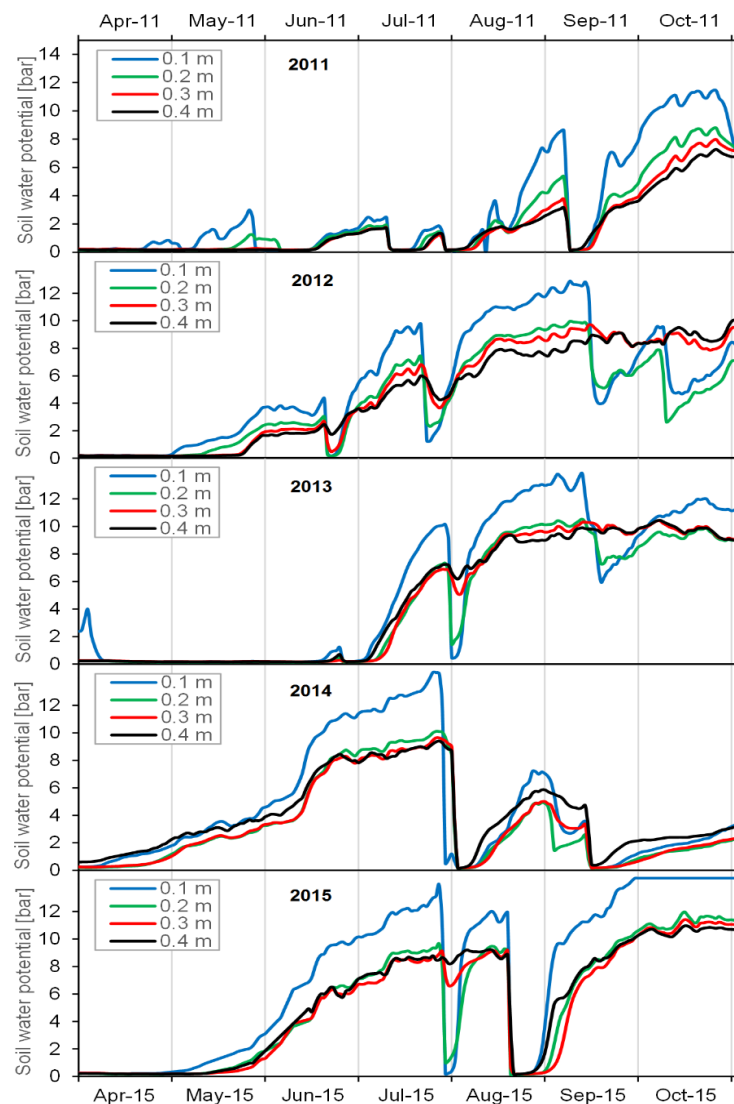


Figure 8: Seasonal course of soil water potential (SWP) profile at throughfall exclusion treatment (R) in depths 0.1, 0.2, 0.3 and 0.4 m. In 2011 and 2012 only 40 % of the plot was covered, since June 2013 70 % was covered which resulted in earlier and more severe incidence of water shortage in seasons 2014 and 2015 at R plot. Note, that SWP is in fact negative, therefore, numbers on y axis represent negative values of SWP.

4.2.2 Above ground biomass productivity

The initial (June 2011) and the final (Oct 2015) standing stocks of control (C) and throughfall exclusion (R) treatments are shown in Fig. 9. Given the start of the 2nd rotation cycle in spring 2009, the initial standing biomass, measured firstly in June 2011, comprised 27.07 ton of dry matter per hectare (DMT ha⁻¹) at C and 25.91 DMT ha⁻¹ at R, respectively. Statistical analysis ANOVA showed no significant effect on initial standing biomass ($p = 0.697$) at different treatments or replications, i.e. the experimental layout was appropriate and initial standing biomass within treatments and among replications (blocks 1, 2, 3) did not differ. The mean annual ABP since resprouting after harvest in early spring 2009 until the beginning of the throughfall exclusion experiment in June 2011 was 10.83 DMT ha⁻¹ yr⁻¹ for controls and 10.36 DMT ha⁻¹ yr⁻¹ for R. The mean annual ABP of first 3 years of the 2nd rotation (2009–2011) prior the establishment of this experiment was 12.31 DMT ha⁻¹ yr⁻¹ for C and 11.60 DMT ha⁻¹ yr⁻¹ for R (including R treatment growing second half of 2011 growing season under 40 % throughfall exclusion treatment). The mean annual ABP for C and R during years 2011–2015 was 12.21 and 11.32 DMT ha⁻¹ yr⁻¹, respectively. The inter-annual ABP was growing until peak ABP was reached in 2013 for C (12.54 DMT ha⁻¹ yr⁻¹) and one year earlier for R (11.65 DMT ha⁻¹ yr⁻¹), representing 5th and 4th year of the 2nd rotation cycle. The ABP then slowly declined to 11.70 DMT ha⁻¹ yr⁻¹ for C, and 10.72 DMT ha⁻¹ yr⁻¹ for R in 2015.

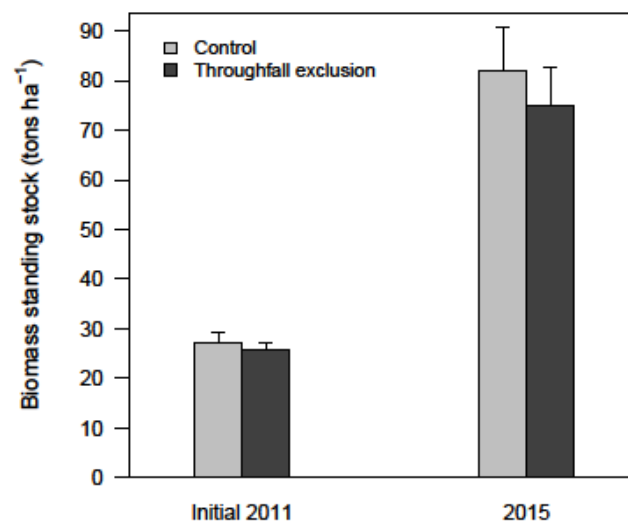


Figure 9: Initial (June 2011) and final (Oct 2015) standing stock of control and throughfall exclusion treatment, expressed in tons of dry matter per hectare.

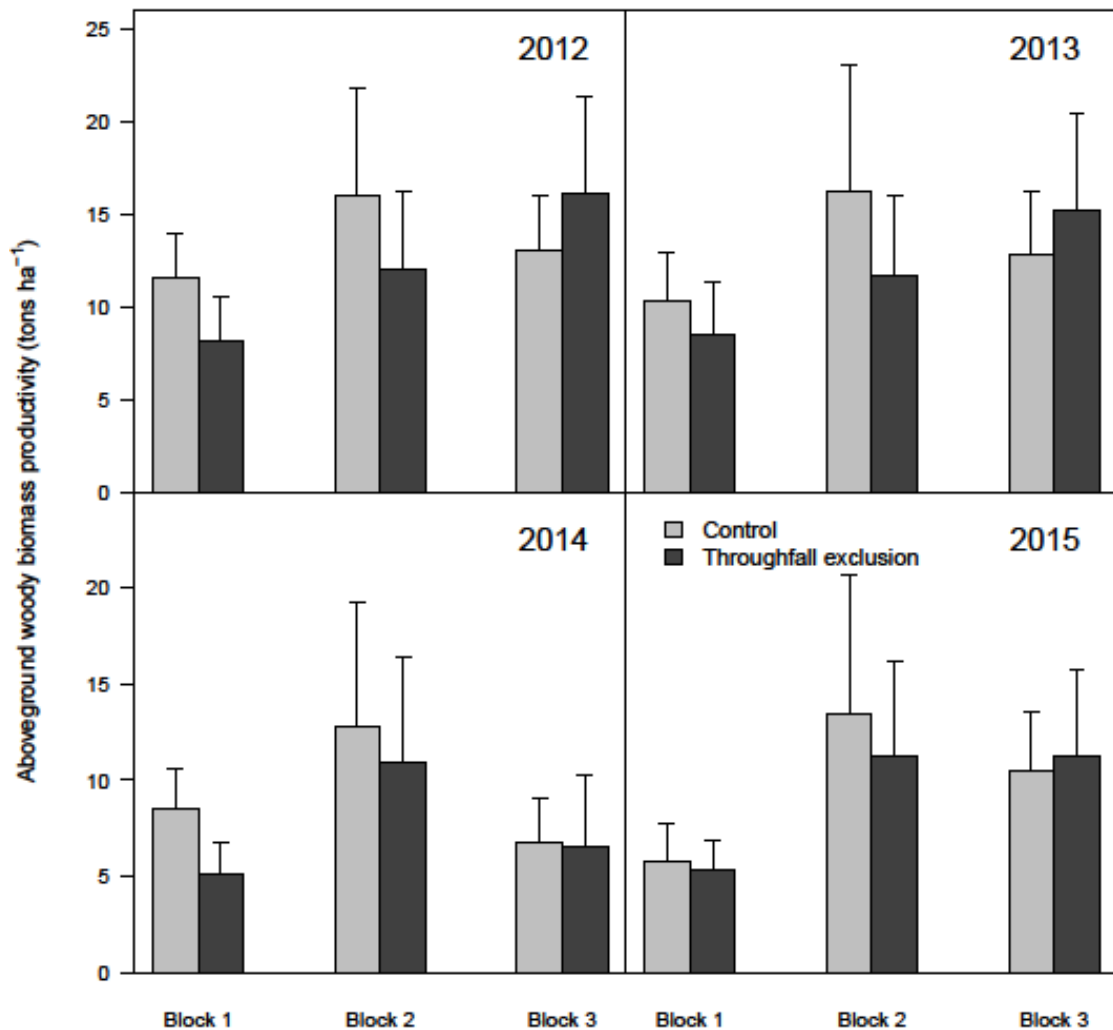


Figure 10: Annual aboveground biomass productivity of control and throughfall exclusion treatments of individual blocks.

The final standing stock at the end of the experiment in Oct 2015 reached 81.87 DMT ha⁻¹ for C treatment, whereas R for treatment it reached 75.02 DMT ha⁻¹, respectively. Thus, the effect of the throughfall exclusion on the final standing stock resulted in 6.85 DMT ha⁻¹, which represents ABP reduction of 8.36 %, not statistically significant ($p = 0.572$). Fig. 10 depicts the annual ABP of C and R treatments, where blocks 1, 2, 3 are shown separately. R treatments at block 1 and 2 showed decreased ABP in all years, what was expected scenario regarding the throughfall exclusion which lowered soil water availability. After 5 years at individual block level, the R treatment caused 18 % and 17 % decrease of ABP at blocks 1 and 2, but 14 % increase at the block 3. In other words, the throughfall exclusion treatment at the block 3 surprisingly

led to 14 % higher biomass production as compared to C treatment. This anomaly will be further elaborated in the discussion section. ABP of block 1 ranged between 5.77–10.36 DMT ha⁻¹ yr⁻¹ for C treatment and 5.34–8.50 DMT ha⁻¹ yr⁻¹ for R, respectively. Generally, block 1 showed the least biomass productivity, hence the throughfall exclusion effect was the most pronounced. The ABP of block 2 ranged between 12.75–16.24 DMT ha⁻¹ yr⁻¹ for C and 10.91–12.05 DMT ha⁻¹ yr⁻¹ for R, respectively. This indicates, that block 2 showed highest productivity. The ABP of block 3 was the most variable and ranged from 6.51–13.0 DMT ha⁻¹ yr⁻¹ for C and 6.58–16.09 DMT ha⁻¹ yr⁻¹ for R. The C treatment at block 3 had lower productivity than R treatment, with one exception in year 2014. Due to an abundant precipitation during growing season 2014, the treatment effect was more pronounced. Because of the variability in ABP between treatments and blocks, the treatment effect on final standing stock was not significant ($p = 0.572$).

4.2.3 Analysis of dominance

The aim of this analysis was to explain considerable variability in ABP among experimental blocks within presented experiment. Binkley (2004) hypothesized that the dominance is related to the pattern of cumulative distributions of stem mass and growth. Trees within particular plot were arranged from smallest to largest (according to DBH) for each time period, and the cumulative distribution for stem mass was compared with the cumulative distribution for stem growth. In other words, relative contribution of each tree to the total growth of the entire plot was quantified. A stand showing no dominance would have 20% of the stand increment produced by the trees that comprise each 20% tile of the stem mass. A stand with strong dominance would have notably more than 20% of the total stand growth contributed by the largest trees that comprise the top 20% of stem mass (Binkley, 2004). As depicted in Fig. 12, each blue and red dot represents a single tree (stem) growing within C and R treatment of respective block. A tree stand with most trees located below the 1:1 line represent positive growth for dominance, i.e. increasing dominance of bigger trees on the account of smaller suppressed trees. This analysis was performed using stem diameter inventory data from year 2011 and 2015. Thus, it was possible to compare the shift in stand composition and dominant patterns of the first (2011) and the last (2015) year of the experiment. In upper part of Tab. 5 there is shown the growth performance of 3 biggest trees of each plot in 2011 and 2015. In other words, it shows how many percent of the total standing

biomass of the particular plot is accumulated in these 3 most dominant trees and how many percent of the annual plot productivity is facilitated by those 3 trees. In lower part of Tab. 5 is similar analysis for the top 1 biggest tree in each plot.

Table 5: *Upper part – relative contribution of 3 biggest trees within particular plot to total stem volume mass and annual stem increment. Lower part – relative contribution of the single biggest tree within particular plot to total stem volume mass and annual stem increment.*

3 biggest trees of each plot	Block 1				Block 2				Block 3			
	C		R		C		R		C		R	
	% of biomass	% of growth	% of biomass	% of growth	% of biomass	% of growth	% of biomass	% of growth	% of biomass	% of growth	% of biomass	% of growth
2011	19	21	26	30	20	31	29	30	19	25	26	32
2015	25	21	34	47	39	60	48	71	29	38	42	53

1 biggest tree of each plot	Block 1				Block 2				Block 3			
	C		R		C		R		C		R	
	% of biomass	% of growth	% of biomass	% of growth	% of biomass	% of growth	% of biomass	% of growth	% of biomass	% of growth	% of biomass	% of growth
2011	7	7	9	9	7	9	12	14	7	10	11	14
2015	10	16	13	13	15	27	17	28	11	18	22	33

Firstly, it illustrates, that in 2011 the total stem biomass volume of 3 biggest trees at C and R treatment comprised 19–20 % and 21–35 % of the total biomass accumulated at particular plot, respectively. Secondly, it shows that these 3 trees facilitated 21–31 % and 30–32 % of annual stem biomass growth at C and R treatments, respectively. In 2015, however, same 3 biggest trees at C already comprised 25–39 %, whereas at R treatment comprised already 34–48 % of total aboveground biomass per plot. In addition, these 3 trees at C and R treatment accounted for 21–60 % and 47–71 % of annual stem biomass increment in 2015.

Regarding the top biggest tree per plot, there can be seen following: in 2011 the largest tree at each one of C treatments comprised 7 % of the total plot biomass, accounting for 7–10 % of the annual growth, whereas at R treatment it comprised 9–12 % of the total plot biomass, accounting for 9–14 % of the annual growth. In 2015 the stem biomass volume of the biggest tree increased at C treatments to 10–15 %, whereas at R treatments it increased to 16–22 %. Moreover, the biggest tree accounted for 16–27 % of the annual growth at C treatments and 13–33 % of the annual growth at R treatments. The absolutely top dominant tree is the tree S1, growing at R treatment of

block 3. By the end of year 2015 this tree accumulated 22 % of the total standing biomass at this plot and accounted for considerable 33 % of the annual growth of the entire plot. In Fig. 11 there is a comparison of tree-frequency distribution in 2011 and 2015. Trees are divided into subclasses for each 10 mm of tree DBH. There can be seen an apparent loss of smaller trees in time, with formation of several dominant trees, especially at block 2 and block 3. This trend is apparent among all experimental blocks, but more pronounced is at R treatments.

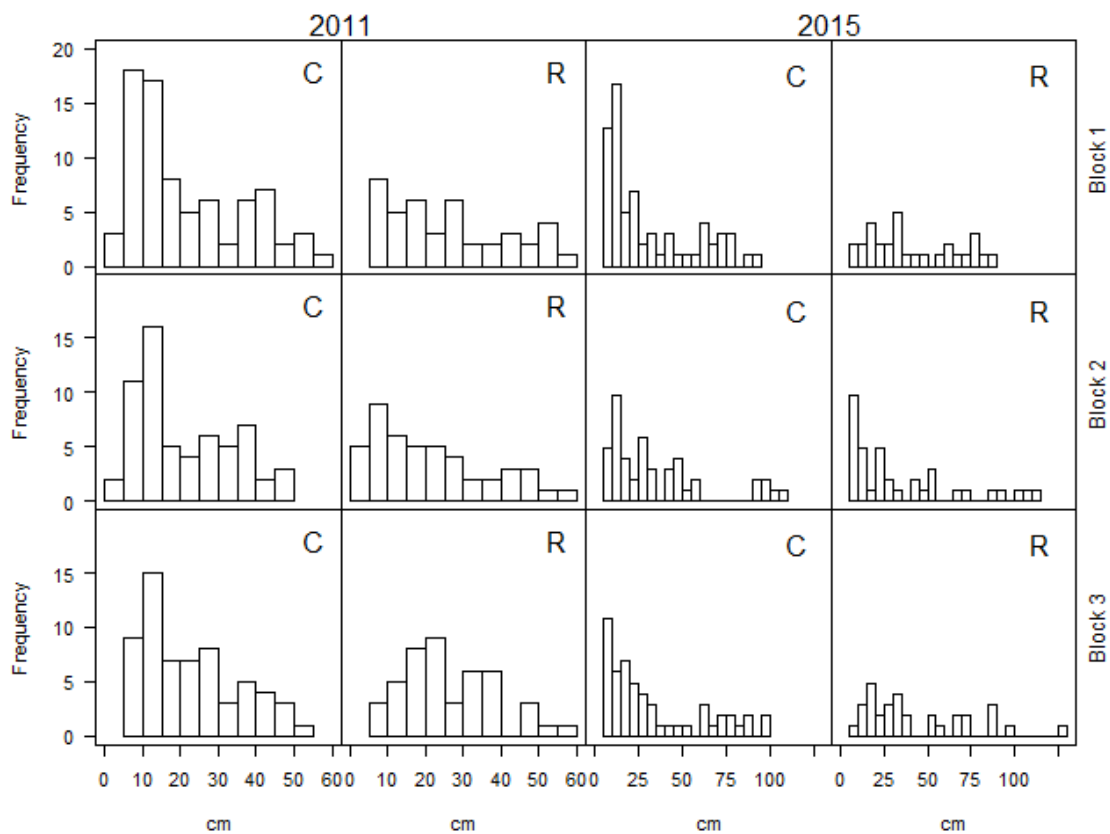


Figure 11: Comparison of tree diameter distribution of control and throughfall exclusion treatments within particular blocks in the beginning (2011) and the end (2015) of the experiment.

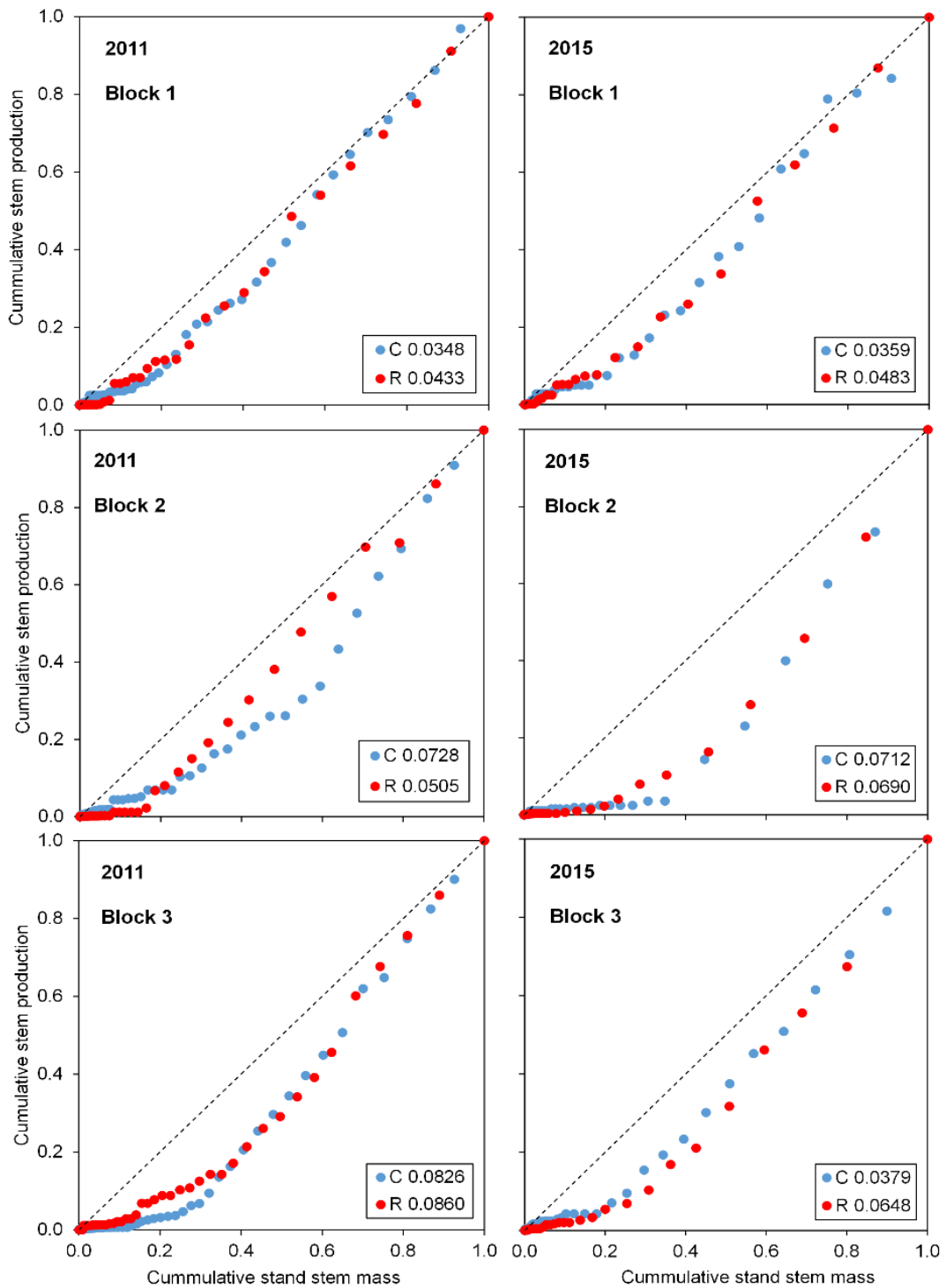


Figure 12: Cumulative distribution of stem mass is linked to the cumulative distribution of stem growth. Each blue and red dot represents a single tree (stem) growing within C and R treatment of respective block. Trees below 1:1 line represent positive growth for dominance. Box in the right-down corner of each graph contains Gini coefficients (Katholnig, 2012), quantifying the heterogeneity of trees within particular plot.

4.2.3.1 Stool mortality

Fig 13. depicts the development of average stool mortality of C and R treatment in period 2011–2015. The average mortality of C treatments increased from 21.2 % in 2011 to 22.9 % in 2015, i.e. change of about 1.7 %. The average mortality of R treatments was lower than C at the beginning of the experiment (20.8 %), but in 2012 it started to rise up to 29.2 % in 2014 and 2015, which represents an average increase by 8.4 %. On Tab. 6 there can be seen considerable variability in stool mortality among blocks 0 to 37.5 %, which was already present at the establishment time of the experiment. Block 3 shows increasing mortality appearing since the year 2012.

Table 6. *Stool mortality (%) at particular block and treatment during years 2011-2015.*

	Block 1		Block 2		Block 3	
	C	R	C	R	C	R
Jun-11	5.0	0.0	28.6	37.5	30.0	25.0
Apr-12	5.0	0.0	28.6	37.5	30.0	25.0
Apr-13	5.0	0.0	28.6	37.5	30.0	31.3
Nov-13	5.0	12.5	28.6	37.5	35.0	31.3
Nov-14	5.0	12.5	28.6	37.5	35.0	37.5
Oct-15	5.0	12.5	28.6	37.5	35.0	37.5

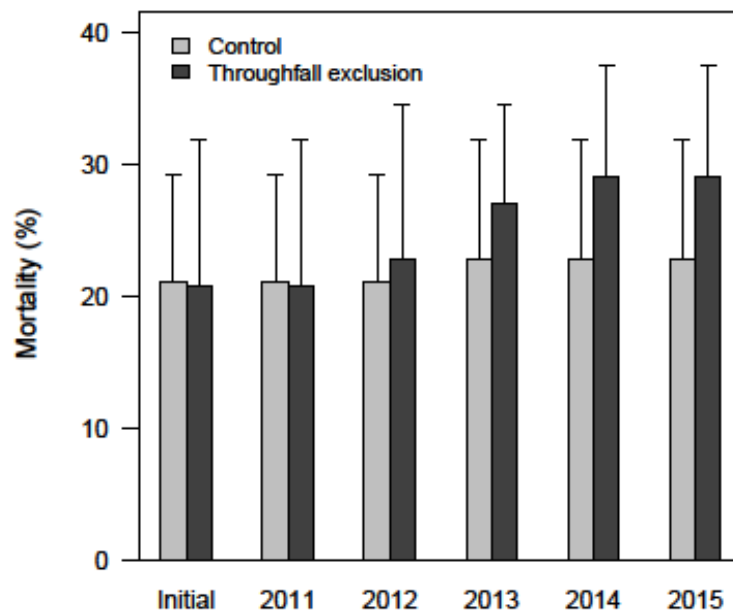


Figure 13: *Stool mortality of control and throughfall exclusion treatment during growing seasons 2011–2015.*

4.3 Discussion

4.3.1 Soil moisture patterns and experimental design evaluation

This is an important part of this thesis explaining the performance of the experimental design by using soil moisture measurements as a comparative metric (Vicca et al., 2012). In addition, this section comments on unforeseen restrictions of this experiment originating from prevailing environmental condition and limitations of this particular experimental site, which could not be managed by such kind of experiment. The purpose of the soil moisture measurement was not entirely an attempt to determine the absolute values at high level of accuracy rather than the tracking of changes in soil water availability among neighboring C and R treatments, as an evidence of the effect of throughfall exclusion treatment (Evetts et al., 2009).

Even though the throughfall exclusion treatment was established already in 2011, first effects on soil moisture started to be apparent as late as in 2013 (most likely result of trenching in June 2012 and increasing throughfall exclusion from 40 to 70 % in June 2013). Nevertheless, the soil moisture status at particular blocks showed high inertia when attempted to restrict it by establishing manipulation experiment. In addition, regardless of throughfall exclusion area percentage, the real change in soil moisture was delayed, unproportioned and not assured. However, the treatment difference was present since year 2013, when drying on R treatments was more pronounced.

Similarly to Hanson et al. (1998), in each year of this study the growing season begun with saturated soils at both treatments. Subsequently, with the initiation of substantial evaporative demand and canopy transpiration in mid-to-late May the R treatment water contents are drawn down faster than those in C treatments. In the drought years of 2015, long periods without rainfall cause treatment differentials to disappear. However, after an abundant rainfall, the treatment differences redeveloped as the soils of control treatments refilled. Substantial impacts of the R treatment on water budget were usually maintained well into November. However, the unforeseen inverse course of soil moisture at block 3 must be discussed at this point, because it affected the averaged-treatment results and compromised statistical evaluation of treatment difference.

Despite the identical size, design and close spatial proximity of experimental blocks within the 1 ha plantation, there were observed considerable different and persistent levels of soil moisture. Presence of significant pretreatment patterns of soil moisture

across the experimental area was also reported by Hanson et al. (1994). It was hypothesized, that the reason is the site micro-topography (Chen a Hu, 2004). The plantation is located on an inclined 8° slope, i.e. the lower edge of the plantation is 8 m below the upper edge. Moreover, the upper edge of the plantation lies on straight line in terms of elevation, whereas the lower edge line is depressed in the center part, thus forming sort of valley. The site-topography resembles an inclined sheet of an office paper, whose lower edge line is bent downwards in the center part. This determines to a big extent the pathways of rainwater displacement and percolation (see Fig. 4B in subchapter Experimental design in section Materials and methods). A decreasing gradient of soil water from the lower to the upper slope positions was also proposed by Mulholland (1993) and the fact, that lower slope positions typically maintain higher water contents caused by gravity drainage of water laterally through the soils was later confirmed by Hanson et al. (1998). Bearing this in mind, author suggests following interpretation to individual treatment performance:

Block 1: *desired and anticipated scenario*. Control and throughfall exclusion treatments are placed at inclined but plane upper part of plantation, with shallow soil; access to ground water is out of question. This resulted in well-developed treatment effect, with an apparent decrease in soil water availability, followed by decreased productivity and water use. On the other hand, the control treatment often suffered from drought stress, as a result of sandy shallow soil, where water quickly percolates.

Block 2: *not-anticipated but acceptable scenario*. Block 2 is located in lower center part of plantation. The soil profile is constantly fed by lateral soil water from upper parts of the plantation (Hanson et al., 2003; Chen a Hu, 2004). Moreover, the soil is deeper as it was washed down from upper parts of the plantation in days, when the area was cultivated as a potato-field. The throughfall exclusion treatment exhibited minor decrease of soil water availability as well, but any severe drought stress did not develop, compared to block 1. This resulted in temporally stable and systematically higher levels of productivity, compared to block 1. Nevertheless, the treatment effect was present, productivity as well as water use of R treatment was lower.

Block 3: *undesired and not-anticipated scenario*. Block 3 has the highest elevation gradient between control and adjacent throughfall exclusion treatment. Although located adjacently next to each other, the control treatment is located upslope towards the southern edge of the plantation, the adjacent R treatment lies downslope towards

the center depression. The R treatment takes advantage of deeper and more humid soil with lateral feeding by water percolating from upper parts of the plantation. Contrarily, the control treatment shows some aspects of water scarcity – lowest seasonal soil moisture (except for year 2014), lower productivity, water use and increased water-use efficiency.

Because the soil moisture patterns were not analyzed prior the establishment of this experiment there was no chance to foresee it. According to abovementioned description, it becomes obvious, that strict sticking to statistical evaluation based on treatments and blocks would not yield any conclusive result, as this experiment was not performed under entirely comparable and controlled conditions (unlike pot experiments or experiments in growth chambers). Future throughfall manipulation experiments should be either established on flat, homogeneous terrain, or soil moisture sampling prior the establishment of the experiment should be performed, in order to identify naturally humid and dry spots (Hanson et al., 1994). Utilizing of such spots could be used for studies, where high soil moisture gradient among treatments is needed. More replications (experimental blocks) would be also appropriate. However, like any experimental design, treatments involve compromises between ideal conditions and logistical reality (Hanson et al., 1994). Additionally, the evaluation should be based on prevailing soil moisture content at particular plot, rather than on presence of particular treatment. Bearing in mind the abovementioned disputation about soil moisture and its naturally occurring patterns, results presented in further chapters make better sense.

4.3.2 Above-ground biomass productivity

This chapter examines the effect of throughfall exclusion treatment (R) on annual above-ground biomass productivity (ABP) of poplar-based short rotation coppice plantation during 3rd - 7th growing season of the 2nd rotation cycle. Triple replicated block design comprised of R treatment and adjacent control treatment (C), which were compared in terms of ABP. Literature sources dealing with similar type of experiment to compare with are scarce, but there can be found some studies which in general evaluated the effect of drought on biomass productivity. These studies were performed either with very similar experimental design but in different climate and plant material (da Costa et al., 2010; Davidson et al., 2008; Hanson et al., 2003; Köhler et al., 2010; Moser et al., 2014; Ogaya a Peñuelas, 2007; Schwendenmann et al., 2010) or in comparable climate but with different plant material or experimental design (D'Orangeville et al., 2013; Dickmann et al., 1996; Linderson et al., 2007; Souch a Stephens, 1998; Ward et al., 2015). Souch a Stephens (1998) subjected 1 year old hybrid clones of *Populus trichocarpa* × *P. deltoides* “Beaupré”, *P. deltoides* × *P. nigra* “Ghoy” and *P. trichocarpa* × *P. trichocarpa* “Trichobel” planted in pots to three levels of drought treatments – well watered, moderate drought and severe drought. According to their results the relative biomass production decreased with increasing severity of the drought treatment. Trees grown in the severe drought treatment produced 60–75 % less dry matter than trees grown in well-watered treatment. Schwendenmann et al. (2010) together with Köhler et al. (2010) performed 3 times replicated throughfall exclusion experiment on cacao and *Gliricidia* agroforestry plantation in Indonesia. The experimental design is very similar to the one presented within this thesis. Within a 1 ha plantation they covered 80 % of projection area of their R treatment by plastic roofs for 13 months. They also made 0.4 m deep drainage trenches around the R treatments and the experiment was three times replicated as ours. They reported 45 % reduction of cacao bean yield at R treatment. On the other hand, Monclus et al. (2006) studied impact of drought on productivity of 29 genotypes of *Populus deltoides* × *Populus nigra* within an irrigated and non-irrigated (drought) treatment near Orleans, France. Trees were planted in pots. They found that productivity across all treatments displayed large genotypic variability and most of the productive genotypes displayed a low level of drought tolerance (i.e. a large reduction of biomass), while the less productive genotypes presented a large range of drought tolerance. This is trade-off between

productivity and drought tolerance was well documented (Bacon, 2009; Boyer, 1982; Dickmann et al., 2002; Kramer, 1962). Wikberg a Ögren (2007) found, that increased allocation of growth resources to xylem conduit and fiber wall thickening will increase resistance to xylem cavitation and, hence, increase a plant's resistance to drought, but on the other hand, it will divert growth resources from leaf growth and thus reduce assimilation and relative growth rate. Similarly, increasing the relative allocation of growth resources to roots will increase drought resistance, but reduce harvestable biomass (Sperry et al., 1994). Attia et al. (2015) studied various stomatal regulations strategies for growth, water-use efficiency, and survival of poplar SRC and found that under high soil moisture, anisohydric hybrid poplar clones had a clear advantage because of their faster growth and higher photosynthetic rates, which may facilitate higher biomass production. As biomass crops are grown on increasingly marginal lands to prevent competition with food production, under these conditions, planting the isohydric hybrids is preferable, because it has high water use efficiency and is able to grow and survive under poorer conditions, although its performance is limited in terms of growth. Linderson et al. (2007) compared the productivity of 6 willow clones grown under non-irrigated rain-fed treatment and contrasting drought treatment. Their throughfall exclusion design comprised of plastic sheeting placed between the rows of trees during 1 growing season) and found considerable variability in yields between clones. Nevertheless, for the dry treatment the productivity was lower for 5 of 6 clones.

Yields of control treatments observed within this experiment were higher than the reported range 7–10 DMT ha⁻¹ yr⁻¹ (Hauk et al., 2014; King et al., 2013; Verlinden et al., 2015). Our results showed annual ABP over 7 years of the 2nd rotation cycle to be 11.7 and 10.72 DMT ha⁻¹ yr⁻¹ for C and R, respectively. Comparing the of productivity on inter-seasonal scale, the peak productivity appeared in years 2012 and 2013, i.e. during 4th and 5th growing season followed by slow decrease in years 2014 and 2015. It might be caused by change in ratio between LAI and tree internal respiration. In contrast to young shoots the older and thicker trees may exhibit higher rates of respiration in proportion to their assimilating leaf area. Nevertheless, it is hard to distinguish, whether this decline in production is caused by environmental factors or rather by genetic traits of hybrid poplar. Either way this finding supports the preference of shorter rotation lengths up to 5 years. Management using 5-year harvesting intervals

should also have the best nutrient efficiency according to González-García et al. (2012) in Nielsen et al. (2014).

Taking into account the block-averaged effect of R treatments, we observed modest response of ABP and considerable variability of ABP across experimental blocks similar to results of Monclus et al. (2006) or Linderson et al. (2007). Given the same microclimatic conditions, monoclonal plantation and experimental design, the source of such variability can be explained by differences in soil water availability among replications which could not be managed solely by the throughfall manipulation experiment. Vicca et al. (2012) published a study about potential shortcomings and common misinterpretations of precipitation manipulation experiments and described a similar situation as was observed within this experiment in case of block 3, i.e. tree with roots penetrating the bedrock to extract considerable amounts of water (Schwinning, 2010), thus complicating the estimation of tree available water and the evaluation of the experiment. However, higher productivity of R treatment (as observed at block 3) is not completely unique example. Ward et al. (2015) performed a 3-year (2012–2014) throughfall exclusion experiment with Loblolly Pine (*Pinus taeda*), which is a widely used species in forestry of South East of US. They applied a throughfall exclusion treatment with roofs at 30 % of the ground area and found a surprising 4% increase of the stem volume at the R treatment. This is in contradiction to the generally accepted opinion that the throughfall exclusion manipulation will reduce stomatal conductance, which further reduces photosynthesis and thus the stem increments (Attia et al., 2015; Ryan, 2011; Zhou et al., 2013). However, in our case, the surprising increase in productivity of R treatment was far more higher (14 %) than relatively negligible 4 % reported by Ward et al. (2015). Such opposite ABP pattern present at block 3, i.e. higher productivity of R treatment compared to C treatment can be explained by two co-occurring reasons. Firstly, the ill-considered position of block 3 within the plantation allowed for access of R treatment to deeper soil layer, which are fed by lateral water inflow percolated from upper parts of the plantation (Hanson et al., 1998; Mulholland, 1993). Thus, the soil water availability of throughfall exclusion treatment was higher than that of control plot, which exhibited lower productivity. However, this water is more easily accessible for larger trees with deeper root system, but not for smaller suppressed trees. Secondly, this situation creates an onset of a very competitive environment and results in formation of few dominant trees, which capture

most of available resources. This has detrimental effect to suppressed trees which further starve, waiting for some kind of external disruption of superiority of the dominant tree. Otherwise, suppressed trees die out providing even more resources to dominant trees, which further thrives (Binkley, 2004; Cavin et al., 2013; Gitlin et al., 2006; Katholnig, 2012). This situation most likely occurred at throughfall exclusion treatment at block 3, what resulted in formation of single “super dominant” tree “S1”, with sinker roots deep below the soil layer, where the soil water availability could not be modified by the throughfall manipulation experiment, such the one presented within this thesis. This issue is discussed in detail in the next section. Bearing this complexity in mind, the resulting message about the different productivity at the particular block can be perceived as diverse responses of poplar plantation to various independent climate scenarios.

Under such perspective the block 1 showed steady response of ABP to R treatment, typical for rain-fed areas; i.e. soil water availability decreased (see Fig 7) and this led to 18 % decreased ABP (see Fig. 10) at R during the duration of this experiment (2011–2015). This scenario was enabled due to the position of the block 1 on upper side of the plantation, with shallow soil, with bedrock outcrops close to the surface of the soil and no access to ground water or any underground stream water at all. Soil water availability at both treatments was determined by precipitation income only. Rain water at Block 1 quickly percolates down to lower parts of plantation, being inaccessible for further use. For instance, in 2014 when seasonal precipitation was highest (417.8 mm) and ET_0 in the same time was lowest (488.4 mm) compared to other years (see Tab. 4), the C treatment received 368.1 mm of throughfall precipitation, whereas R only 110.4 mm. The treatment effect became more apparent. The ABP of control treatment was supported by throughfall precipitation whereas the ABP of R treatment showed decrease in ABP by 41 %. Contrarily, in very dry and warm year 2015, the seasonal precipitation was lowest (290.5 mm) and ET_0 was highest (560.4 mm) compared to period 2011–2015. The C treatment received 202.7 mm while R only 60.8 mm. Given the high air temperature and ET_0 both treatments starved for water, soil moisture same at both treatments was low which was reflected in decrease in productivity of both treatments (C treatment – 5.78 DMT ha⁻¹ yr⁻¹, R treatment – 5.40 DMT ha⁻¹ yr⁻¹) as reported by Hanson et al. (1998). The ABP reduction was only 6.48 % at R treatment, because both treatments suffered from severe water stress. This is most likely

a simulation of the worst future climate scenario, with much higher temperatures and lower precipitation amounts. This results suggest a good drought resistance of hybrid clone J-105. Despite an adverse climatic conditions this clone can effectively control its water loss via stomata aperture and still maintains certain level of productivity.

Block 2 resembles scenario of SRC grown on deeper humid soil, receiving water laterally, similar to riparian ecosystems where trees of *Populus* genotype generally thrive. It provides an insight to a range of a potential attainable yields, if this clone is planted in fertile soil with good soil water availability. Block 2 showed long-standing higher levels of soil moisture and also the ABP was highest compared to Block 1 and block 3. Even so, the throughfall exclusion effect was present and decreased the ABP on average by 17 % during 2011–2015.

Block 3 worked differently, than expected. Drawing any suggestion regarding behavior of SRC plantation under future climate based on the results of block 3 might be inappropriate, as it worked exact opposite. However it demonstrated the soil moisture heterogeneity and allowed to gain an insight into principles driving manipulation experiments and in such context this result represents valuable experience, which will be reflected in design and interpretation of future manipulation experiments.

4.3.3 Analysis of dominance

In order to evaluate changes in the stand composition between treatments and replications over multiple years an approach based on Binkley (2004) was adopted. According this approach two patterns are observed in the development of most even-aged forests: trees differentiate into various dominance classes (Oliver a Larson, 1990), and overall forest growth increases, peaks, and then declines (Ryan, 1997). These two patterns are driven by a host of interacting processes, including: the supply and use of resources (such as light, water, and nitrogen), competition for resources, and differences in the efficiency of trees (and species) in using resources to grow. According to Binkley (2004) the decline in stand-level wood productivity that commonly occurs shortly after canopy closure may be driven primarily by shifts in dominance among trees, and by the ensuing declines in efficiency of resource use by the suppressed trees. Short rotation coppice plantation is a good example of such even-aged forest stand where trees are forced to compete for resources due to high planting density. The decline in stand-level growth near canopy closure is driven by increasing dominance of larger trees, leading to declining efficiency of resource use by smaller trees. With further stand development,

the ability of large trees to dominate smaller trees declines as the spacing between trees increases, and large, old trees enter a phase where their growth no longer keeps pace with their increasing dominance of site resources. Although, this situation should not occur in SRC with shorter harvest rotations, considerable heterogeneity of stand composition was observed within all blocks of this study, with higher heterogeneity at R treatments. It was hypothesized, that the throughfall exclusion treatments decreased soil water availability and thus enhanced competitive relationships between trees at R treatments (Binkley, 2004; Cavin et al., 2013; Katholnig, 2012; Pretzsch a Schütze, 2015). This resulted in higher mortality and disappearance of smaller trees (see Fig. 11) and formation of several dominant trees thus utilizing more resources. This is distinctly apparent at R treatments of block 2 and block 3. This approach was also adopted to explain exceptional of R treatment at block 3, where biomass productivity in throughfall exclusion treatment was surprisingly higher compared to control treatment. This trend was present in all years (2011–2015), except year 2014, when an abundant precipitation enhanced the soil water availability and ABP of C at block 3. This reversed treatment effect on ABP was to certain extent caused by the extraordinary large tree S1, which was growing in the center of the throughfall exclusion plot at block 3. This tree was growing at some sort of “sweet spot”, in terms of higher soil water availability (caused by deeper roots compared to neighboring suppressed trees). In addition, due to its supreme position and larger canopy, this tree received also higher doses of stemflow water, which was quantified as 14 % of gross precipitation at this site (Orság et al., 2013a). This resulted in high transpiration rate due to well-irradiated canopy and access to lateral soil water (the highest transpiration rate among all trees within presented study was observed at this tree) resulting in rapid growth despite the throughfall exclusion treatment. The tree S1 in 2015 accounted for 33 % of the annual biomass growth at this plot and the stem volume of this tree comprised 22 % of total standing biomass at this plot. It also was the thickest tree (DBH 123.6 mm in July 2015) within this study across all blocks. High mortality of 37.5 % at this plot and an absence of similar dominant trees to compete with allowed this tree to gather more resources and grow faster. Based on abovementioned evidence it was assumed that this tree was the major reason of high ABP estimates and reversed treatment effect at the block 3.

4.3.3.1 Stool mortality

Generally, the lowest mortality was observed at block 1, the highest (although constant) at block 2. The highest increase in mortality occurred at R treatment of block 3, which is in good agreement with the analysis of dominance from previous chapter (Binkley, 2004). High mortality levels at block 2 did not increase nor decrease during the duration of this experiment. It is a result of lower living-stump density resulting from poor re-sprouting after the first harvest in 2009. On the other hand it decreased competing for resources within this block and allowed for formation of smaller number of dominant trees.

4.4 Conclusion

This experiment attempted to simulate an effect of future drier climate on above-ground biomass productivity (ABP) of an operational poplar-based short rotation coppice (SRC). During the 2nd rotation cycle (2009–2015), the ABP reached 81.87 tons of dry biomass per hectare (DMT ha⁻¹) at control treatment (C) and 75.02 DMT ha⁻¹ at treatment with throughfall exclusion manipulation (R), which was established between years 2011–2015. The treatment difference in terms of ABP was 6.85 DMT ha⁻¹, representing statistically non-significant ($p = 0.342$) reduction in ABP of 8.36 %. The average annual ABP during the 2nd rotation cycle reached 11.7 and 10.72 DMT ha⁻¹ for C and R treatment, respectively. The highest annual ABP was reached during the 5th year of growth (2013). All three experimental blocks of C and R treatments showed considerable variability in soil moisture patterns and corresponding ABP. The R treatment of the first and second experimental block successfully decreased soil water availability during growing seasons 2011–2015, what resulted in 17.5 % decrease in ABP at R, compared to C. At block 1 the ABP ranged between 5.77–10.36 DMT ha⁻¹ yr⁻¹ for C and 5.34–8.50 DMT ha⁻¹ yr⁻¹ for R, respectively. The ABP of block 2 ranged between 12.75–16.24 DMT ha⁻¹ yr⁻¹ for C and 10.91–12.05 DMT ha⁻¹ yr⁻¹ for R, respectively. This block showed highest productivity. The third experimental block, performed the opposite, as there were observed higher levels of soil moisture at R compared to C, which were most likely caused by the position of the R treatment downslope from C, in more humid soil environment. The ABP of block 3 was the most variable and ranged from 6.51–13.0 DMT ha⁻¹ yr⁻¹ for C and 6.58–16.09 DMT ha⁻¹ yr⁻¹ for R. The initial (2011) stool mortality ranged between 5–37.5 % depending on particular plot. This was most likely caused by an unequal re-sprouting after the harvest in 2009. The mortality increased by 1.7 and 8.4 % at C and R, respectively, during growing seasons 2011–2015. To explain heterogeneity of tree size within particular plot an analysis of dominance was performed. It revealed strong tendency to competitive relationships between neighboring trees and increased growth of dominant trees on the account of smaller trees, causing their eventual dieback. This led to formation of few dominant trees, comprising ~30 % of the total biomass at particular plot, accounting for ~50 % of the annual increment per 25 m² plot. This tendency was more pronounced at R treatments.

5 CHAPTER II.: ANALYSIS OF DECREASED SOIL WATER AVAILABILITY ON WATER USE

5.1 Introduction

5.1.1 Plant water relations

Over that part of the earth's surface, where temperatures permit plant growth, the occurrence of trees is controlled chiefly by the water supply. The ecological significance of water arises from its physiological importance. An adequate supply of water is just as essential to the successful growth of plants as photosynthesis and the other biochemical processes involved in the synthesis of food and its transformation into new tissues (Larcher, 2003). The importance of water to a plant lies in its role in cell expansion, cooling of leaves, nutrient and carbon transport, photosynthesis, and as a solvent or reagent in key metabolic reactions. Water limits growth more than any other environmental variable (Dickmann et al., 2002; Mittler, 2006; Niinemets, 2010). An essential factor in plant water relations is maintenance of an amount of water sufficient to sustain cell turgor and permit normal functioning of the physiological and biochemical processes involved in growth. Plant water status is controlled by the relative rates of water absorption, water loss, and internal storage (Larcher, 2003).

A crucial step in the colonization of terrestrial environments by plants has been the evolution of mechanism that enable plants to control their water loss while continuing to fix carbon dioxide in photosynthesis. This step has been so important because the availability of water is probably the key factor determining plant distribution and survival in natural ecosystems. All those mechanisms that tend to maintain plant survival or productivity under conditions of limited water supply or high evaporative demand can be described as a drought tolerance mechanisms. It is clear, that drought tolerance have corresponding "costs", in terms of reduced net productivity or competitive ability, because the pathway for CO₂ uptake through stomata is also the main route for water loss in transpiration. Therefore, any stomatal closure acting to conserve water will have a corresponding inhibitory effect on potential yield (Bacon, 2009). The importance of water in the life of woody plants can be shown by listing it's more important functions, which can be grouped in four categories: 1) Water is an essential constituent of protoplasm and forms 80 to 90% of the fresh weight of actively growing tissues. 2) Water is the solvent in which gases, salts, and other solutes move

within and between cells and from organ to organ. 3) Water is a reagent in photosynthesis and a substrate or product in many other metabolic reactions. 4) Water is essential for maintenance of turgidity of cells and tissues, assuring the presence of a driving force for cell enlargement, stomatal opening, and maintenance of the form of young leaves and other slightly lignified structures (Dickmann et al., 2002; Larcher, 2003; Pallardy, 2010). Water can move from the soil, through the root and stem, to a transpiring leaf only if there is a continuity of liquid throughout the pathway. In addition to continuous columns of water in the xylem, the plant also requires continuity of liquid water in the capillaries of the soil and the tissues of root and leaf. Water moves through the soil-plant-atmosphere system in response to differences in its free energy content, which decreases progressively as the water flows from the soil, through the xylem and the leaf to the bulk air. Thus, the water flows from the soil through the plant to the air in response to gradients in free energy (Fitter and Hay, 2001). In a freely transpiring plant rooted in a soil at field capacity, water evaporates from the moist cell walls of epidermal and mesophyll cells in the interior of the leaves and is lost to the atmosphere via stomata. As water loss proceeds, the water potential in the leaf apoplast falls below that of the leaf cells, and also below the water potential in the xylem and the soil. Water is, therefore, withdrawn from neighboring leaf cells, causing a lowering of cell water potential and wilting (Fitter and Hay, 2001).

5.1.2 Sap flow

Studies of plant-water relations often require the flux of water through the plants to be known. Measurement of the water flux is commonly made at the leaf or shoot level using chamber measurements, such as gasometry or porometry (e.g. Licor 6400XT, AP4 Delta-T Devices). However, these methods have severe limitations when the measurements have to be scaled up to the stand level. Stand-level estimates of water use by forest trees are often obtained using micrometeorological approaches such as the Bowen ratio energy balance (Fischer, 2012) and eddy flux methods (Burba, 2013; Meinzer et al., 2001). On the other hand, measurements using micrometeorological methods at the stand level ideally require large homogeneous areas and flat terrain (Cienciala et al., 1992). If we decide to use micrometeorological methods for this experiment, each treatment would need at least one square hectare of flat homogeneous area. Considering number of treatments (2) and replications (3) then a plantation of about 6 ha would be needed. It is therefore difficult to design experiments in which the

effect of different treatments in respect of supply of water, nutrients or soil acidification on plant water relations can be studied. In this context, it is desirable to measure the total transpiration or water uptake of single trees (Cienciala et al., 1992). Recent refinements and simplification of sap flux measurement techniques have made it economically feasible to measure whole-tree sap flow as a surrogate for transpiration in a relatively large number of trees simultaneously (Granier, 1987; Meinzer et al., 2001). Nowadays, sap flow measurements are routinely used with leaf-level measurements to investigate the relative importance of stomatal and boundary layer conductance in controlling canopy transpiration, whole-tree hydraulic conductance, coordinated control of whole-plant water transport, movement of water to and from sapwood storage, and whole-plant vulnerability of water transport to xylem cavitation (Wullschleger et al., 2001). Further, sap flow estimates provide a specific estimate of transpiration, as opposed to total evaporation, thereby minimizing additional experimental measurements or analysis required to isolate this component (Hatton et al., 1995). Energy-balance, heat dissipation and heat-pulse methods can be used to compare transpiration in different parts of a watershed or between adjacent trees, or to assess the contribution of transpiration from overstory and understory trees. Such studies often require that rates of water use must be extrapolated from individual trees to that of stands and plantations (Wullschleger et al., 1998). In following subchapters are described several operations necessary for successful scaling of tree sap flow into the stand transpiration.

5.1.2.1 Sapwood area determination

According to usual physiological terminology, the sapwood (or hydroactive xylem) is located in the outer part of the xylem conducting sap and the heartwood (or inactive xylem) is the inner non-conducting xylem (Čermák a Nadezhdina, 1998). In non-technical terms, a cross section of a tree consists of bark on the outside, phloem, xylem or wood in the center, with a thin growing layer of vascular cambium between them. All of the cells of the xylem, with the exception of the ray cells in the sapwood and those still differentiating within about 1 mm of the cambium, are dead. As new increments of xylem are formed at the cambium, metabolic waste products that are toxic or inhibitory to live cells are translocated toward the center of the tree where they accumulate to cause death of parenchyma ray cells to form heartwood. The portion of xylem, which lies between the cambium and the heartwood, which contains tracheary elements and

living parenchyma ray cells, is called sapwood. Sap flow does not occur in the heartwood, neither does sap flow occur in the immature and differentiating tissue just inside the cambium, nor in the latewood portion of each growth ring (Swanson, 1994). Sapwood cross-sectional area is a simple biometric parameter widely used for scaling the transpiration data between trees and forest stands. If all trees had the same type and arrangement of sap conducting tissue, the task of sap flow measurement and scaling of transpiration would be relatively easy. Unfortunately, they do not (Köstner et al., 1998; Swanson, 1994). It is known that the extent of the conducting role of sapwood area is different according to species, ontogenetic phases and environmental conditions (Čermák a Nadezhdina, 1998; Kozłowski a Pallardy, 2002; Kramer, 2012; Wullschleger a King, 2000).

5.1.2.2 Scaling sap flux density to transpiration

There is widespread interest in the use of sap flow measured on single trees to derive estimates of canopy transpiration and forest water use. Such extrapolation requires not only accurate measurements of sap flow, but also detailed inventories of stand-level attributes including tree domain, defined either by distance between stems or crown area (Hatton a Vertessy, 1990), basal area, leaf area or sapwood area (Hatton et al., 1995). Each of these attributes has been used with varying success to estimate canopy transpiration (Kume et al., 2010; Vertessy et al., 1997; Vose et al., 2003; Wullschleger et al., 2001). However, in practice, few studies use more than a single attribute to extrapolate sap velocity to the canopy scale.

Many investigators currently describe areal rates of forest water use as the product of sap velocity and stand sapwood area. Allometric relationships between stem diameter or circumference and sapwood area are typically established based on increment cores or stem disks taken across a range of size classes. Total sapwood area is estimated by applying these equations to inventory-based assessments of individual tree diameter or circumference in a stand (Tsuruta et al., 2010; Vertessy et al., 1995; Wullschleger a King, 2000). Although extrapolations based on sapwood area are conceptually simple, estimates of tree and forest water use derived in this manner are subject to uncertainties (Köstner et al., 1998; Kume et al., 2010; Smith a Allen, 1996). Foremost among these uncertainties is the actual proportion of sapwood functional in water transport. It is important, therefore, that strategies for sampling sap flow account for variation in

transpiration within the tree stand (Čermák et al., 1992). Where members of a stand population vary primarily in size, sap flow for individual plants can be scaled to stand transpiration by determining relationships between sap flow rates and stem diameter, stem basal area, sapwood area or leaf area and then extrapolating transpiration rates to unit area of land on the basis of surveys of tree size or measurements of leaf area index (Allen a Grime, 1995; Clausnitzer et al., 2011; Vertessy et al., 1995).

5.1.3 Transpiration

Transpiration is an evaporative process at the surfaces of a plant whereby water is lost from the soil via a plant's water conducting system (Slatyer, 1967). The process of transpiration involves water movement through the soil, roots, stems, and leaves into the atmosphere in response to water potential gradients, always moving in the direction of smaller potential or negative gradients (Vose et al., 2003). Transpiration takes place through the stomata which are present on the leaves of the plant and is called stomatal transpiration. Of the total amount of transpiration from the plants about 80 % to 90 % transpiration is leaves the plant via the stomata (Vose et al., 2003). Transpiration consists of the vaporization of liquid water contained in plant tissues and the vapour removal to the atmosphere (Allen et al., 1998). It mainly depends on the weather, soil water conditions, leaf area index and physiological activity, accordingly, it varies a lot day to day (Lindroth a Báth, 1999).

5.1.4 Water use efficiency

Water use efficiency (WUE) of crop plants can be defined as the amount of water taken into a plant in order to produce a unit of output, where output may be total biomass or biomass assigned to a harvestable crop (Bacon, 2009). Water use efficiency is considered instantaneous when it refers to the ratio of instantaneous fluxes of carbon dioxide and water vapor (Dickmann et al., 2002; Lindroth a Cienciala, 1996). It can also be defined as the ratio of CO₂ assimilation into photosynthetic biochemistry to water lost, via transpiration, through the stomata. WUE is not constant value and can be increased when water is limiting. Assimilation and transpiration are regulated by stomatal conductance to water and CO₂ and the respective concentration gradients in water vapour and CO₂ between the inside and outside of the leaf. Under any particular set of conditions, the driving force for CO₂ uptake will be enhanced by lowering CO₂ concentration inside the leaf, while the driving force for water loss will remain relatively unchanged, leading to an increase in WUE (Bacon, 2009).

5.2 Methods

5.2.1 Sap flow

A measurement of the ascent of xylem sap in a tree trunk has many implications in various scientific fields. Taken over a sufficiently long time period, the quantity of sap flow upward through the stem must equal transpiration from the leaves. The occurrence of transpiration indicates that stomata are open, a necessary condition for gas exchange during photosynthesis (Swanson, 1994). This is why several methods for field measurement of the ascending water flow (sap flow) through a plant stem (or branch, root) cross-section have been established during the last 40 years (Čermák et al., 1973; Granier, 1987; Kučera et al., 1977; Sakuratani, 1984; Swanson, 1994).

5.2.1.1 Sap flow methods overview

Transpiration of whole tree, stems or branches can be determined using various techniques ranging from monitoring soil moisture loss, vapor loss to the surrounding atmosphere, or liquid flow through the plant stem, i.e. xylem sap flow; which is most frequently used (Čermák et al., 1973; Kramer, 2012; Vose et al., 2003). All methods commonly applied for sap flow measurement are based on the same physical principle – monitoring quantity or quality of a tracer, applied into xylem tissue, carrying the information about moving sap. A certain part of conductive woody tissue is heated and heat dissipation is assessed from temperature measurements in two locations of the plant stem (or branch, or root), namely in the heated domain and outside the heated domain (Tatarinov et al., 2005). The earliest attempts used simple relationships between the first onset of an induced heat pulse measured at one or more points downstream in the stem from the heat induction site. This was followed by a compensation technique in which heat flow in both the upstream and downstream directions was detected to allow for conduction, as well as advection of heat from one point to another. Lastly, stem anatomy was considered mathematically and various sap velocity (heat pulse velocity) and sap flux methods (thermal heat balance) were proposed to place quantitative thermometric methods on a sound physical and theoretical base (Swanson, 1994). The scientific interest in measuring transpiration to study plant water relations is long-standing. The first quantitative measurements of water loss from plants appear to have been made by Stephen Hales, prior to 1727. He measured water loss by weighing potted grapevines, apple and lemon trees, and various herbaceous plants (Swanson, 1994).

Before 1900, some water balance studies treated plant transpiration as a residual term, deduced by subtracting rainfall interception, soil water storage changes, and surface runoff from rainfall (Bosch a Hewlett, 1982; Moran a O'Shaughnessy, 1984). This catchment water balance approach to estimating plant transpiration resulted in considerable uncertainty because such estimates were affected by errors in all of the other measurements (Vose et al., 2003; Wullschleger et al., 1998). Other way of estimating sap flow was application of dyes to trace sap flow in stems and roots, which has been practiced since the beginning of the 20th century (James a Baker, 1933; Kramer, 1940). However, as this method necessitates plant cutting to follow the ascent of the dye, less destructive alternatives were demanded and sought (Vandegehuchte a Steppe, 2013). Huber (1932) was one of the first to report the use of *heat as a tracer* to determine sap flow. He developed the heat pulse method to measure xylem water velocity, which was based on applying heat into xylem tissue. By measuring the time it took for a heat pulse to reach a certain distance downstream from the heater, a measure for sap flow was obtained (Schulze et al., 1985; Vandegehuchte a Steppe, 2013).

The application of thermal methods to the problem of measuring sap flow in trees is relatively simple in practice but complex theoretically. Heat transport in the xylem sapwood of a tree stem occurs by convection in the flowing sap and by diffusion through the sap as well as the stationary tissue of both the sapwood and heartwood. Tiny temperature changes or gradients in the order of 10ths of degrees Celsius must be detected with certainty in a thermally noisy ambient environment. Physiological processes of growth and defense against pathogens add complexity (Vandegehuchte a Steppe, 2013). There are two broad methodological categories: heat pulse methods, which use pulses of heat as markers in the sap stream, and heat balance methods, which measure the components of heat transport from a continuous heat input (Edwards et al., 1997). Moreover, a distinction must be made between heat balance methods measuring sap-flow rate (g h^{-1}) (i.e. stem heat balance – SHB, tissue heat balance – THB method), determining the total sap flow in a plant stem or stem section, and those measuring sap-flux density ($\text{g m}^{-2} \text{h}^{-1}$) (heat dissipation), assessing the amount of sap flowing through a certain cross sectional area per time. The former are very useful for estimating whole-plant water use, but they are less suited to investigation of variation in sap flow within the plant, e.g. radial sap-flow (Vandegehuchte a Steppe, 2013).

Sap-flow rate can be measured by either the SHB or THB method. Both methods solve the heat balance over a stem section of the plant during continuous application of heat to the tissue, applying a constant or variable power (Smith a Allen, 1996). Among methods, measuring sap flux density belongs “thermal dissipation” (TD) method and “heat field deformation” (HFD) method. The early work on transpiration of trees was summarized by Raber (1937), Slatyer (1967), Swanson (1994) or Smith a Allen (1996). Others, like Köstner et al. (1998), Wullschleger et al. (1998), Bush et al. (2010), Steppe et al. (2010) or Vandegehuchte a Steppe (2013) present discussions of various methods of measuring transpiration and their advantages and disadvantages. For purposes of this study one method from the group of heat balance methods was chosen – the heat dissipation method, based on Granier type sensor (Granier, 1987).

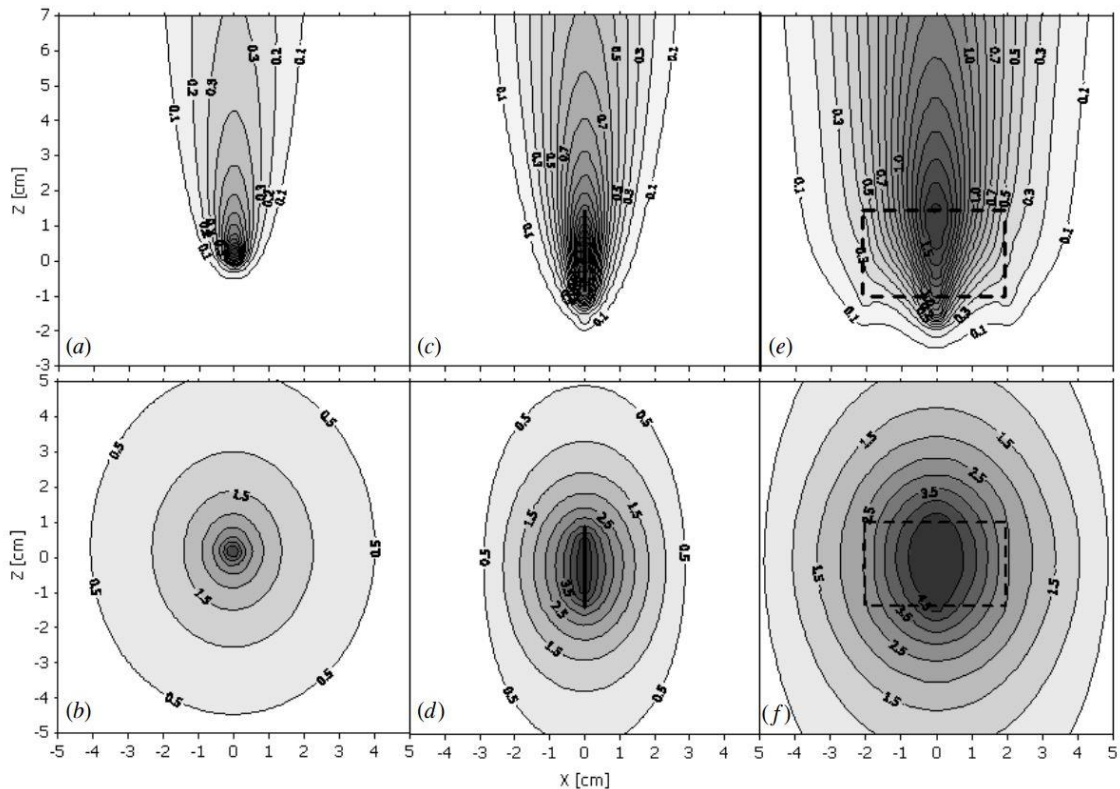


Figure 14: *Typical configurations of simulated temperature field (tangential cross-section 1.5 cm from stem surface) for needle (a), (b), plate (c), (d) and volume (e), (f) heating for sap flow 0 (a), (c), (e) and 30 (b), (d), (f) $g\ cm^{-2}\ h^{-1}$. Bold segments (c), (d) and rectangles (e), (f) present heated domain (Tatarinov et al., 2005).*

5.2.1.2 Heat dissipation method

The heat dissipation method introduced by Granier (1985, 1987) measures sap velocity as the temperature difference between heated and unheated probes inserted radially into the stem (Granier 1985, 1987). The technique is particularly popular among tree physiologists and forest hydrologists owing to its simplicity, high degree of accuracy, reliability, and relatively low cost (Clearwater et al., 1999; Lu et al., 2004). The measuring element (sensor) consists of two needle probes 20 mm long and 2 mm in diameter (see Fig. 16). Probes are radially inserted into the pre-drilled hole into the sapwood of the trunk at distance of approximately 125 mm from each other. Each one contains a T-type copper-constantan thermocouple inserted in the middle of each probe's central tube. The diameter of the thermocouple wire is 0.125 mm. The distal 20 mm of each probe is wrapped in a coil of insulated constantan wire, and the upper (downstream) probe is constantly heated by applying a known voltage across the heating element, giving a constant power output of 0.2 W, while the lower probe is considered as temperature reference. The thermocouples are joined at the constantan side. The temperature difference signal between the probes is transferred to a datalogger via copper leads. The temperature difference signal can be recorded and processed as raw sensor output in millivolts (mV) or it can be transferred to degrees Celsius (Kelvin). The Granier equation works equal in both ways.

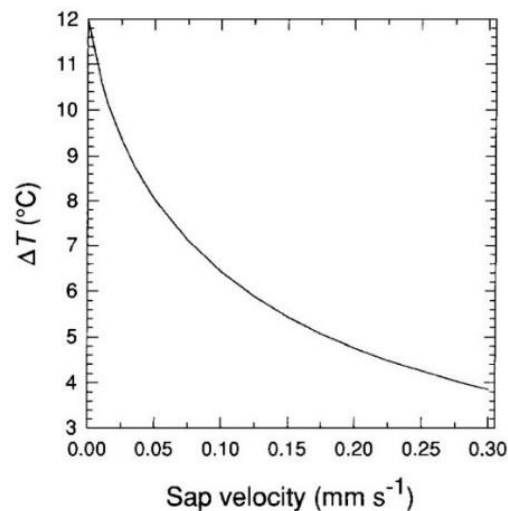


Figure 15: The temperature difference (ΔT) between the heated and unheated probe as a function of sap velocity (Clearwater et al., 1999).

Heat dissipation increases and the temperature difference between the heated and unheated probe declines asymptotically with increasing sap velocity (Fig. 15). The intensity of the electric current in the heating element of the sensor is fixed to 0.1 A (for an average value of the resistance of the heating element of 20 Ω , the heating power is 0.2 W) (Lu et al., 2004). Each sensor, i.e. heated and reference probe were installed approximately 10 – 15 cm in the vertical distance. Unlike the heat pulse method, the distance is not critical as long as the reference probe is not influenced by the heated probe.

Each sensor was installed at the northern side of the tree trunk and wrapped around by an insulating foil with reflective cover in order to minimize the influence of naturally occurring thermal gradients in the stand or solar irradiation. Each sensor was connected to the datalogger with a 4 wire cable, 2 wires carrying signal other 2 wires for energy supply for heating coil inside the heated probe. Heating elements of 4 sensors were connected in serial. This was later found as a shortcoming, because if any short circuit or damage happened to any of fine heating wire, whole group of 4 sensor were out of service. Considering the number of sap flow sensors at all replications (18), there was 72 wires connected with the total length of 450 m. Each sensor, comprised of heated and reference probe was installed approximately 1.3 m above ground.

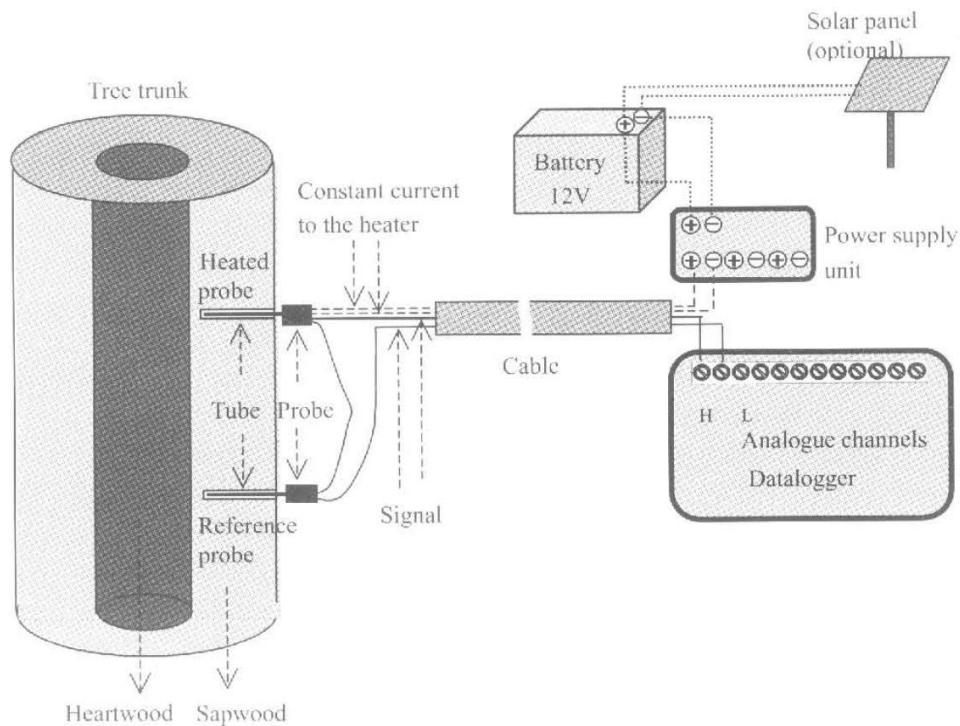


Figure 16: Configuration of Granier-type system for sap flow measurement (Lu et al., 2004)

5.2.1.3 Determination of maximum temperature difference

The determination of maximum temperature difference (ΔT_{\max}) is fundamental precondition for the calculation of F_d . The parameter ΔT_{\max} can theoretically be determined as ΔT at $F_d = 0$ (Lu et al., 2004). This situation means absence of xylem water flux, which usually occurs at predawn. In early morning the trunk water storage depleted by daily transpiration is already refilled and usually the evaporative demand of atmosphere (VPD) is low. Thus the ascent of sap through xylem ceases and there is no water flow left, which could move the heat from heated probe further upwards. This particular moment of zero flow state sometimes takes only minutes and is called the ΔT_{\max} parameter. From that reason a program script for Mini32 software was developed. This program was inspired by approach of Oishi et al. (2008). The program helps to determine ΔT_{\max} based on course of VPD overnight. If the average VPD is lower than 0.2 kPa over at least 6 hours during night, the scripts takes ΔT record for 3 AM and considers this value as ΔT_{\max} . This so called VPD condition allows to determine ΔT_{\max} of multiple sensors in a standardized and fast way. Nevertheless, there is still need for visual control and eventual adjustment, as the program does not consider precipitation and other meteorological factors, which might shift ΔT_{\max} .

5.2.1.4 Sap flux density

Sap flux density was calculated according to original equation proposed by Granier (1985):

$$F_d = 0.119 * \left[\frac{(\Delta T_{\max} - \Delta T)}{\Delta T} \right]^{1.231}$$

where F_d stands for sap flux density ($\text{Kg m}^2 \text{s}^{-1}$, i.e. kilograms of water passing through 1 m^2 of conductive sapwood per 1 second), ΔT is temperature difference measured between the unheated and unheated probes at given F_d , ΔT_{\max} represents the maximum temperature difference established between the heated and non-heated probes at zero flux ($F_d = 0$), 0.119 and 1.231 are empirically derived parameters proposed by Granier (1985). The mass flow of sap was calculated as shown in Eqn. X:

$$Q = F_d * A,$$

where A (m^2) is the cross-sectional area of the sapwood calculated as the ring area centered and F_d is the sap flux density (Meinzer et al., 2006).

5.2.1.5 Gap filling

There are different ways of handling missing data, but the most common is using linear regressions between sensors if any of them are working and only use environmental covariates to fill gaps when no sensors are working (Ward 2014, personal communication).

With the help of programmer Bc. Jan Balek a software named “Gap filling” was developed. It is based on Delphi programming language. The program uses one of four preset linear regression equations to fill gaps in sap flux density data. It can be applied to any kind of variable where it is appropriate, any time step, but it was mainly developed for sap flux datasets with multiple sensors. It can process as much as 20 channels simultaneously. In such case, for one channel which is processed at the moment the software calculates 19 variants of linear regression parameters with all remaining 19 channels. Then the program selects regression parameters with the highest correlation coefficient and uses it to fill the gap. For the sake of appropriate function the daily course of global radiation and precipitation amounts are considered for calculation. There are several options, which must be fulfilled before the regression is calculated: (i) “radiation threshold” (global radiation of min. $50 \text{ W m}^{-1} \text{ s}^{-1}$), (ii) precipitation threshold, (iii) “minimum (number of) values for regression”, (iv) “maximum days interval” – search window can be limited to a preset number of days before or after the gap, (v) “values for regression before gap (%)” – percentage of total amount of values within the gap, which will be searched preceding the gap and used for calculation of regression parameters. If the gap contains 100 values and the parameter is set to 70%, then program takes 70 values before the gap and 30 values after the gap. There are two variants - the latter is used, if it rains during the gap (default is 100%, i.e. all values are for calculation are searched before the gap starts).

Table 7: *Example of input file for gap filling.*

YEAR	DOY	TIME	GRAD	PREC	Ch1	Ch2	Ch3	Ch4	Ch5	Ch6
2013	121	0:10	0	0	-9999	0.00123	0.00484	0.00023	0.00185	0.00037
2013	121	0:20	0	0	-9999	0.00114	0.00461	0.00021	0.00171	0.00012
2013	121	0:30	0	0	-9999	0.00104	0.00439	0.00019	0.00156	0.00018
2013	121	0:40	0	0	-9999	0.00094	0.00428	0.00017	0.00142	0.00016
2013	121	0:50	0	0	-9999	0.0009	0.00356	0.00016	0.00136	0.00015

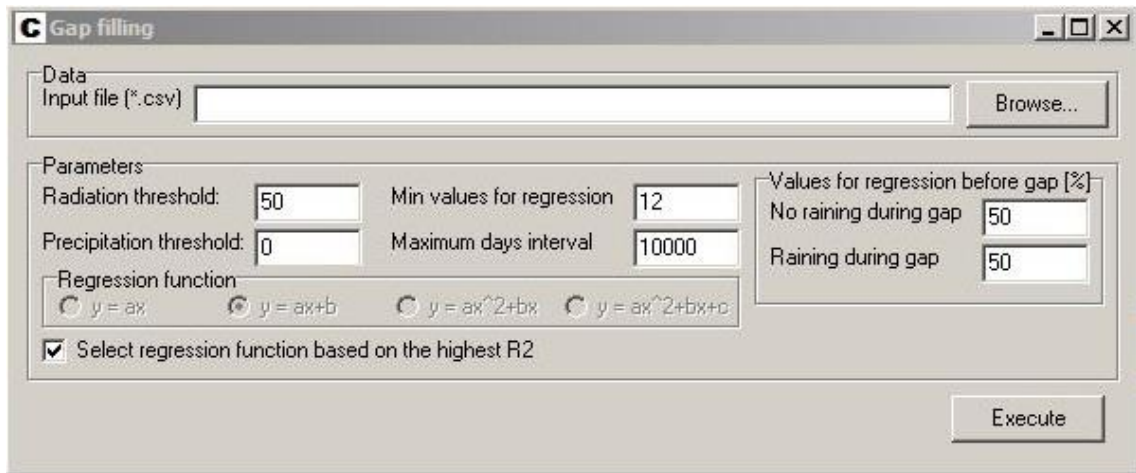


Figure 17: *Gap filling software – user interface.*

Input data file is comma separated file with columns in given order (see Tab. 7). After successful gap filling the program creates a log file for each channel. This file contains all regression parameters used and percentage of gap size filled with specific regression parameter. At last, joint log file is created, where the final percentage of filled gaps is summarized.

5.2.1.6 *Sapwood area determination*

There are many ways to determine sapwood area. Coring tree ring samples with an increment borer, applying dye into holes pre-drilled in stem and subsequent destructive cutting stem into segments and seeking for traces of dye in the cross sectional area, computer tomography, or resistance to penetration (Rust, 1999). To address this question a parallel experiment within SRC plantation was established in mid June 2013. The experiment was designed to answer question how the sap flux density changes in opposite azimuthal directions (north x south) and how the sap flux density varies in different xylem depths (outer x inner sapwood). Five dominant trees of DBH between 84.3 - 113.6 mm were chosen. Each tree was equipped with an array of 4 heat dissipation sap flow sensors, according Granier design. Two sensors measured outer ring (0 – 2 cm) of xylem from northern and southern side of the trunk. Other two sensor measured inner ring (2 – 4 cm) of xylem from northern and southern side of the trunk, same as previous two sensors. Measurements were taken each minute and 10 minute averages were stored at datalogger CR1000 (Campbell scientific). Sensors were wired to multiplexer AM16/32 (Campbell Scientific), which was connected to CR1000. The measurement campaign lasted whole summer 2013.

5.2.1.7 *Scaling of sap flow to transpiration*

Granier sap flow sensors measure tree water use by measuring the density (velocity) of water flowing up the xylem (i.e. sap flow density). This number must be multiplied by the area of the conductive sapwood, in order to calculate the volume of water moving up the stem per unit time (i.e. sap flow rate). The challenge is how to use this single estimate of a volume flux moving up one tree, to provide a larger-scale estimate of stand water use. Scaling water use to the whole-tree or stand-level based on either sap flow method is limited by the accuracy with which the sapwood or functional xylem area, and the radial variation in sap flux density can be determined. An appropriate way to scale limited measurements of tree water use by some scalar of tree size, knowing the distribution of that scalar for the entire stand (Vertessy et al., 1995). Scaling of tree water use in monospecific stands such as poplar plantation can be reasonably straightforward applying accurate determination of sapwood area–tree size relationships and representative measurements of sap flow in relation to tree size and sapwood depth (Čermák et al., 1995; Hatton et al., 1995; Köstner et al., 1998). In this thesis transpiration was calculated using extrapolation of an average sap flux density of 3 trees within each experimental plot to millimeters of water column per unit of projection area (1 m²). In this way, scaling was based on combination of sap flux density data and cross sectional area of all trees, presented in particular experimental plot. The cross sectional area of all trees within particular plot was calculated according to annual stand inventory measurement. The number of treatment (2 – control and throughfall exclusion) and the number of replication (3 – block 1, 2, 3) gives six independent scaling procedures and thus six transpiration calculations. Within each experimental plot 3 sap flow sensor were installed, thus each plot-related transpiration calculation resulted from sap flux density data, based on averaged measurement of 3 sensors.

5.2.2 *Water use efficiency*

Water use efficiency was obtained by dividing the harvestable of biomass production (DMC) in g per m² of the projection ground area by the amount of transpired water, expressed in millimeters of water column per m². The WUE was defined from harvestable part of above-ground woody biomass – stem and branches, while leaves and roots were not considered, as it would require more extensive research to quantify it. The water use efficiency was determined on a tree level (2011) and on stand level (2012 – 2015).

5.3 Results

5.3.1.1 Determination of maximum temperature difference

Daily fluctuation of temperature difference (ΔT) is the main proxy information for sap flux calculations. Given the constant heating current 100 mA (i.e. 0.2 Watt) the rate at which the temperature dissipates is determined by thermal properties and water content of wood surrounding the probe (Lu et al., 2004).

On Fig. 18 is depicted an example of daily course of ΔT , measured by 2 randomly selected sensors. There can be seen that ΔT between upper heated and lower reference thermocouple has magnitude of approximately 3 – 5 degrees Celsius. Note that ΔT might also be expressed in Kelvins (Vandegehuchte a Steppe, 2013), but in this thesis degrees Celsius is used. However, a tree with high sap flow density (F_d) would have even bigger magnitude of ΔT and contrarily a tree with low F_d would have narrower range of ΔT resembling a flatter curve. As mentioned in the methodology section, for determination of maximum temperature difference (ΔT_{\max}) a new calculation procedure (program) for Mini32 software was created and tested. It was based on a simple condition: if vapor pressure deficit (VPD) during night stays at least 6 h below 0.2 kPa then the ΔT_{\max} is reached. Low VPD during night suggests, that transpiration most likely ceased or was negligible due to low evaporative demand of atmosphere and the length of 6 h is needed because it is considered as a sufficient time for a tree to refill the internal water storage. The program was able to identify approximately 60 points of ΔT_{\max} over 5 months of growing season, i.e. one point per 2.5 day, depending on VPD. The procedure worked well, but still it needed a lot of attention, as it did not take into account the daily course of VPD, precipitation events and soil water availability, which might shift ΔT and thus ΔT_{\max} upwards or downwards (as a result of different water content in woody tissue, thus changing the dissipation of the heat). After careful adjustment the ΔT_{\max} points were linearly interpolated, so that each value of ΔT had an appropriate value of ΔT_{\max} . All datasets of ΔT of all years of the experiment duration were processed in such way in order to ensure consistency of methodology.

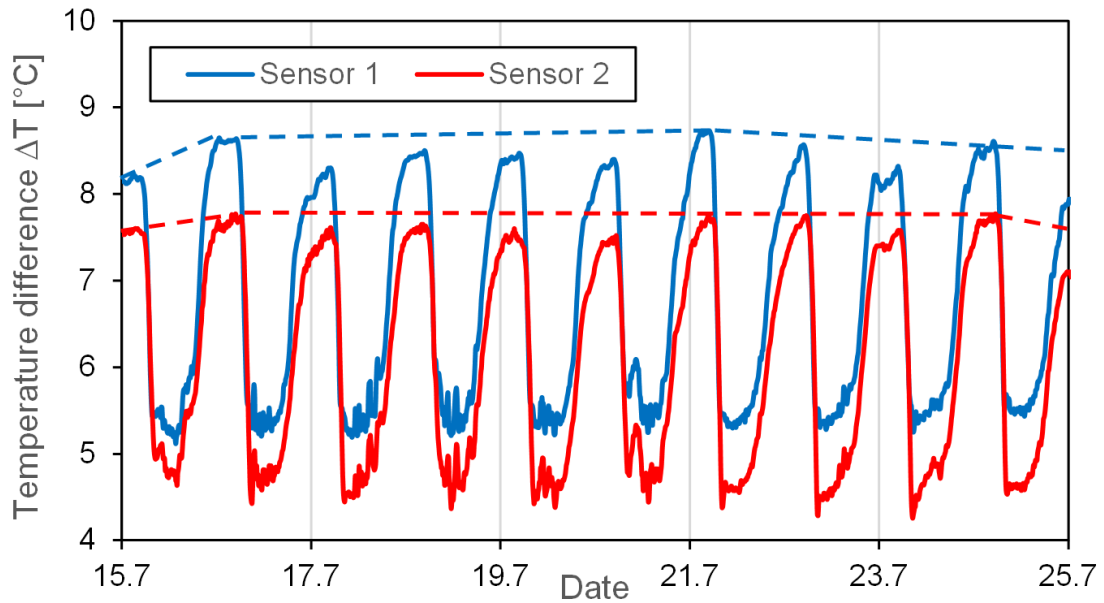


Figure 18: An example of daily course of temperature difference (ΔT) of 2 randomly selected sensors (solid lines) in summer 2013. Dashed lines represents daily maximum temperature difference (ΔT_{max}), which are used for calculation of sap flux density (F_d).

5.3.1.2 Sap flux density

Having the ΔT correctly measured and the ΔT_{max} reasonable determined, the calculation of sap flux density is a straightforward and easily automated task. Sap flux density (F_d) was calculated according to the original Granier empirical equation (Granier, 1987) as described in section Methodology. Dataset of 10 minute averages of temperature difference, measured in degrees Celsius each minute was combined with maximal temperature difference (interpolated to 10 minute step as well) and thus the F_d of in sapwood depth 0–20 mm was obtained for each tree. All datasets 2012 – 2015 were calculated identically. On tree level, daily maximum of F_d ranged from 15–117 $\text{cm}^3 \text{m}^2 \text{s}^{-1}$ depending on tree size, soil water availability, VPD and irradiation. In 2012 F_d was highest in late May with daily maximum 25–55 $\text{cm}^3 \text{m}^2 \text{s}^{-1}$ depending on tree. In 2013 the peak F_d occurred in late June with maximum values 16–98 $\text{cm}^3 \text{m}^2 \text{s}^{-1}$. In 2014 peak F_d occurred in mid-July with daily maximum 23–120 $\text{cm}^3 \text{m}^2 \text{s}^{-1}$. In 2015 the maximum values of F_d 10–121 $\text{cm}^3 \text{m}^2 \text{s}^{-1}$ occurred in first week of June and then kept declining until the mighty rewetting storm event on August 18th (81.6 mm). Summary of F_d on treatment level is depicted on Tab. 8. Lower values of F_d can be

observed in comparison between R and C treatments. Note, that the R treatment average is affected by the exceptionally high F_d of tree S1, growing at R treatment of block 3. From that reason, comparing seasonal median values of F_d might be more reasonable. In such comparison, we can see decreased F_d at R treatments compared to controls by 24.5, 20.1, 9.3, 30.2 and 21.1 % for growing seasons 2012, 2013, 2014, 2015 and 2011–2015.

Table 8: Seasonal summary of F_d ($cm^3 m^2 s^{-1}$) in terms of mean, median and maximal values averaged per treatment

Year	C			R		
	AVG	MED	MAX	AVG	MED	MAX
2012	10.6	10.4	49.4	8.3	7.7	39.8
2013	14.3	14.9	75.3	12.4	11.9	74.3
2014	11.1	10.7	70.1	11.2	9.7	62.6
2015	8.7	9.4	68.6	8.5	6.5	59.7

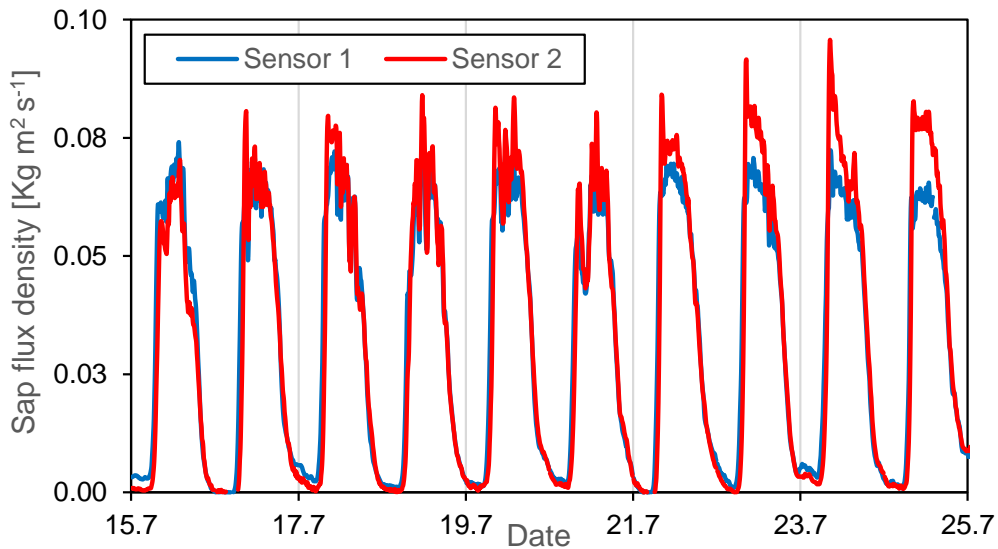


Figure 19: An example of daily course of sap flux density (F_d) of 2 sensors, calculated according to ΔT and ΔT_{max} , from previous Figure.

5.3.1.3 Gap filling

Long term measurement of sap flow depends on a proper functioning of meters of thin electric wires connecting sensor thermocouple with datalogger and sensor heating coil with source of constant electric current. When such setup is exposed to harsh natural environment, occasional gaps in sensor signal are almost unavoidable. The most frequent cause of measurement failure is: (i) external mechanical damage to wires,

(ii) junction failure due to high moisture, (iii) electric failure of datalogger or source of constant electric current, (iv) loss of power (electrical shortcut or empty batteries), because each system was powered by 12 V DC lead acid batteries, which had to be replaced on regular basis. Gap filling was especially needed in year 2013, when 3 dataloggers CR10 (Campbell Scientific, UK) were used for monitoring sap flow instead of 3 dataloggers V16 (EMSBno, Czech Republic). Because all 18 sensors from three DL CR10 working on blocks 1–3 were installed on the same hybrid poplar clone and all trees were exposed to same environmental conditions, the sap flux density data of all 18 sensors were pooled together in order to facilitate gap filling. Performing regression among 18 sensors in Excel would be very time inefficient, therefore a new software called “gap-filling” tool was developed. In case of gap in the data string the algorithm used best linear regression fit between other working sensors to fill the gap. The working principles in details are described in the Methodology section.

5.3.1.4 Sapwood area determination

Total cross-sectional area per 1 ha as determined from annual stand inventory measurements reached 9.65, 15.83, 18.45, 20.77 and 22.93 m² in years 2011, 2012, 2013, 2014 and 2015, respectively.

The determination of the conductive xylem (sapwood) profile of a tree is a complicated task which can result in large errors in sap flux calculation, when improper estimates of sapwood area are adopted (Tatarinov et al., 2005). To address the issue of non-uniform sap flux density in deeper layers of xylem, the sap flux density of five dominant trees was measured in the outer (0–2 cm) and the inner (2–4 cm) circle of the xylem during growing season of the year 2013. Moreover, identical array of sensors was installed from southern and northern side of the tree trunk, in order to track possible differences in azimuthal variations of sap flux density (hereinafter “S/N” ratio). Five dominant trees with DBH between 84.3–113.6 mm growing in the center of the plantation were selected. Note, that in April 2013 all stems within the throughfall exclusion study, which includes block 1, 2 and 3 comprised of 506 stems, with maximum DBH of 82.6 mm and average DBH of 25.8 mm. The sap flux density measurement within this sub-experiment started in mid June 2013 and lasted till the end of September.

Fig. 20 shows typical daily F_d calculated as an average sap flux density over 14 days period. It is evident, that F_d of inner part of the stem is lower than that of the outer diameter. If we relate the average outer F_d , measured by northern and southern sensor to the average inner F_d measured by northern and southern sensor, then we obtain ratio 0.24, i.e. sap flux density in the inner circle is only 24 % of the sap flux density measured in the outer circle. The averaged S/N ratio of all trees was very close to 1, with 14 day period extremes of about 1.76 (Tree 2) and 0.39 (Tree 3). Tree #1 had seasonal S/N ratio 0.83, with STD 0.06, i.e. F_d at northern side of the tree trunk was 13 % higher. Tree #2 started the experiment with similar S/N ratio on both sides. Since July the F_d at the southern side started to prevail and seasonal average S/N ratio exceeded the F_d at northern side by 46 %, i.e. the seasonal S/N ratio reached 1.46 with STD 0.26. Tree #3 performed the opposite direction and reached average F_d at northern side 42 % higher than that measured at southern side (S/N ratio 0.58, STD 0.13). Tree #4 showed the smallest variation with seasonal average of 0.95 with STD 0.07. Tree #5 had the seasonal S/N ratio 1.30, with STD 0.21. Note, that tree #5 had consistently the lowest F_d among sampled trees, although its DBH was 108.2 mm, i.e. near the center of the DBH range of sampled trees. Contrastingly, the tree #4 with DBH 84.3 mm maintained similarly high F_d as trees #1 and #2 with DBH over 113 mm. It means that an assumption, that trees with bigger diameter must necessarily have higher water use than thinner trees is not always valid. In this case we can be quite confident in it, as this finding is based on data from 4 sensor at each tree, measuring throughout the entire sapwood. To conclude, the average ratio between southern and northern F_d measured at all 5 trees ranged from 0.91 to 1.08 with seasonal average value 1.01 and standard deviation 0.06.

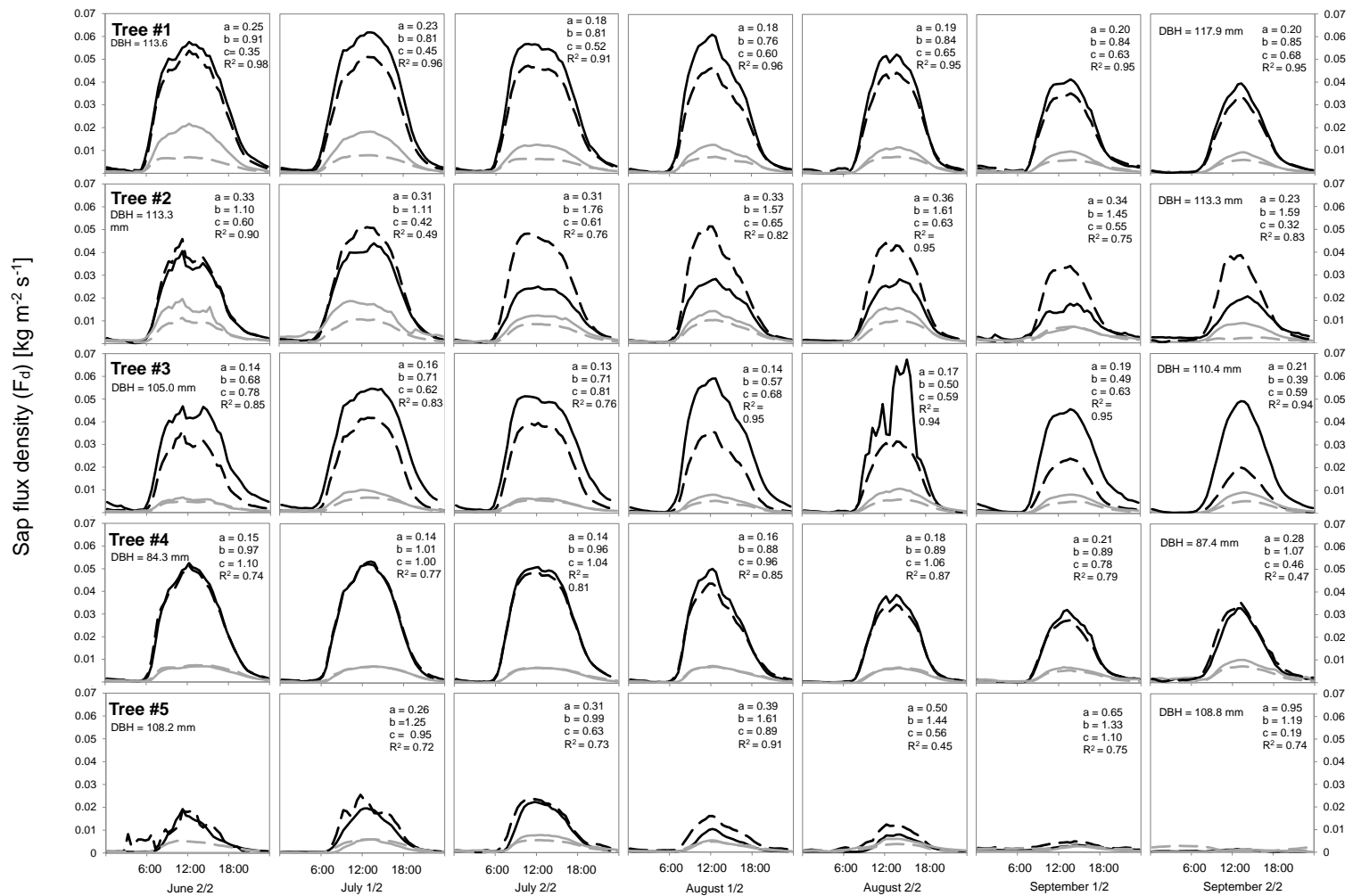


Figure 20: Average sap flux density (F_d) of an average day over 15 day period, as measured by 4 sensors installed at different orientation of a tree circumference and different sapwood depth. The black solid line represents sensor installed from northern side of a tree, measuring in the outer sapwood ring (0–20 mm). The black interrupted line represents sensor installed from southern side, measuring in the outer sapwood as well. The grey solid line stands for sensor installed from northern side, measuring in the inner sapwood ring (20–40 mm). The grey dashed line is sensor installed from southern side, measuring in the inner sapwood as well. Parameter a = ratio of average inner versus average outer F_d , parameter b = ratio of average outer F_d measured from northern and southern direction, parameter c = ratio of average inner F_d measured from northern and southern direction.

5.3.2 Sap flow

Sap flux measurements were performed throughout growing seasons 2011–2015 using heat dissipation method according to Granier (1987), in order to get more detailed information about the water use on a tree level. However, after solving of some methodological issues in first years, the final frame of measurement scheme was implemented in 2013. From that reason some graphs include growing season 2012, whilst other do not. Sap flow datasets analyzed within this study contain sap flow of 18 trees monitored more than four complete growing seasons in high temporal resolution (10 min data). As the demonstration of such dataset exceeds extent of this thesis, the sap flux data were treated into the form of daily totals, seasonal totals, seasonal averages and extremes and were linked to grass-reference evapotranspiration as a baseline co-variable. Data in Tab. 10 compare sap flow of particular trees in periods July–September of years 2013–2015. The seasonal measurements of sap flow started usually up to one month after the bud burst occurred and took place until the loss of foliage in late October. The climate during growing season 2013 had growth supporting trend. Seasonal precipitation (April–October) reached 386 mm, while ET_0 total reached 552 mm. Precipitation in the spring period April–June amounted 191 mm and was well distributed in time, ET_0 was 231 mm, what enhanced sap flow rates. In summer (July–September) precipitation amounted 161 mm and ET_0 291 mm. The mean daily sap flow of trees growing in control treatments (C) was 4.48 kg per tree day⁻¹, whereas trees grown under throughfall exclusion treatment (R) attained sap flow totals of 4.97 kg per tree day⁻¹, suggesting that trees growing under R treatment had a higher water uptake. Note, that this average value of was outbalanced by tree S1, growing in R treatment of block 3, which represented the thickest and largest tree within this study and exhibited exceptionally high sap flow rates in all years; more than twice higher than all other trees. If the tree is omitted, the mean daily sap flow of trees within R treatment would be more realistic 3.72 kg per tree day⁻¹. The maximum rates of sap flow were reached on July 23rd, when an average tree in C treatment used 7.17 kg per day⁻¹ and 8.34 kg day⁻¹ for an average tree in R treatment, respectively (6.03 kg day⁻¹ for tree at R when omitting tree S1). Maximum daily sap flow in year 2013 was observed at abovementioned tree S1 (DBH 98 mm) which transpired 26.64 kg during this day. To compare, the lowest sap flow rate in the same day showed tree S11 (DBH 44 mm) in R treatment of Block 1 with 1.0 kg day⁻¹. This tree suffered partly from water stress,

due to the effect of throughfall displacement treatment and partly due to its suppressed status among surrounding trees. The total sap flow of an average tree in C reached 404 kg, whereas tree from R treatment reached 449 kg (336 kg excluding S1) for period July to September 2013.

Table 9: Comparison of daily mean sap flow (kg), seasonal sap flow totals (kg) and diameter (mm) at breast height (measured at 130 cm) of particular tree during period July–September in years 2013–2015. Horizontal bars represent relative range of particular value compared to the maximum value within each column. Note the tree S1 (bottom line) which exhibited exceptionally high sap flow rates in all years.

Treat.	Block	Tree	2013			2014			2015		
			DBH	Daily AVG	Total Kg	DBH	Daily AVG	Total Kg	DBH	Daily AVG	Total Kg
C	Block 1	K5	74	8.0	721	84	5.8	534	85	4.6	415
		K9	61	4.9	446	68	1.6	149	70	2.0	182
		K3	54	4.0	359	61	2.1	190	63	2.7	245
R	Block 1	S9	77	5.1	462	82	3.6	327	84	3.0	276
		S11	44	0.8	72	46	0.2	21	46	0.1	11
		S6	57	2.9	259	60	0.9	83	61	0.9	78
C	Block 2	K11	77	5.3	482	93	7.1	654	101	5.0	455
		K12	73	5.6	503	84	5.2	481	91	3.9	359
		K13	43	1.0	90	43	0.5	49	109	5.1	463
R	Block 2	S2	73	4.3	391	88	3.0	273	90	3.6	328
		S8	50	1.7	153	52	1.0	92	53	0.6	54
		S11	67	4.5	405	71	3.8	351	71	3.2	292
C	Block 3	K1	77	6.8	614	93	4.1	376	95	1.8	164
		K11	56	2.6	232	62	2.1	191	63	2.2	200
		K6	50	2.1	191	54	1.2	108	55	1.2	113
R	Block 3	S7	64	3.1	278	69	1.8	164	71	1.6	148
		S11	68	6.4	579	83	3.1	287	88	1.9	177
		S1	98	15.9	1439	124	12.7	1168	128	17.1	1563

In 2014 the seasonal precipitation reached 418 mm and ET_o was 512 mm. The difference in daily mean sap flow between C and R treatments became more pronounced, as the effect of the increased roof coverage (from 40 % to 70 % in mid June 2013) at R treatment appeared. Moreover, the spring in 2014 was much dryer compared to year 2013. Precipitation amounted only 129 mm during the April–June period. Note, that 27.2 mm from the total 129 mm fell during a single storm event as late as on June 25th. Thus, trees at both treatments had to deal with water stress during sensitive spring months May and June, when most of the stem growth occurs. The daily mean tree sap flow reached 3.33 kg day⁻¹ for C treatment and 3.35 kg day⁻¹ for C and R treatment (without tree S1 the average for R treatment would be 2.21 kg day⁻¹ per tree). The summer was milder though, with 260 mm rainfall and 235 mm of ET_o .

The maximum rates of sap flow were reached on July 7th, when an average tree in C treatment used 5.77 kg day⁻¹ and 6.16 kg day⁻¹ for an average tree in R treatment, respectively (4.25 kg day⁻¹ with tree S1 excluded). Maximum daily sap flow in year 2014 was observed on July 13th at tree S1 (DBH 124 mm), which transpired 21.34 kg during this day. Contrarily, the lowest sap flow rate in the same day showed tree S11 (DBH 46 mm) in R treatment of block 1 with 0.25 kg day⁻¹. The total sap flow of an average tree in C reached 303 kg, whereas tree from R treatment reached 307 kg (203 kg excluding S1) for period July to September 2014. Dry year 2015 further decreased sap flow rates and exposed trees at both treatments to severe water stress. While the seasonal (April–October) precipitation amounted only 291 mm, the ET_o in the same time reached 588 mm. April to June precipitation resulted only in 88 mm with ET_o of 265 mm. July to September precipitation added only 185 mm (82 mm out of total 185 mm came during single storm event on August 18th), ET_o reached 301 mm, average temperature was 17.5 °C and VPD 0.8 kPa, indicating strong evaporative demand of atmosphere. The mean daily sap flow per tree reached 3.16 kg day⁻¹ and 3.56 kg day⁻¹ for C and R treatment, respectively (without tree S1 the average for R treatment would be only 1.86 kg day⁻¹ per tree). Ten days prior the storm sap flow rates were lower by 42 % compared to average sap flow rate in period July–September, the mean daily temperature was 23.7 °C, with daily maximum reaching 33 °C and daily maximum VPD reaching 3.4 kPa. On August 17th the mean daily sap flow of trees in C treatment was 1.23 kg day⁻¹, whereas for trees in R it was 2.79 kg day⁻¹ (0.78 kg day⁻¹ excluding tree S1). Interestingly, in the same day the tree S1 maintained high sap flow rate of 18.8 kg day⁻¹. The maximum sap flow rates were reached on July 3th, then the trend was decreasing until the end of the season. The mean tree sap flow rate in C treatment reached 5.62 kg day⁻¹ and 11.9 kg day⁻¹ for an average tree in R treatment, respectively (4.06 kg day⁻¹ with tree S1 excluded). Maximum daily sap flow in year 2015 was observed on July 13th at tree S1 (DBH 128 mm), which transpired 28.97 kg day⁻¹. The lowest sap flow rate in the same day showed tree S11 (DBH 46 mm) in R treatment of Block 1 with 0.80 kg per day. The total sap flow of an average tree in C reached 288 kg, whereas tree from R treatment reached 325 kg (170 kg excluding S1) for period July to September 2015. To conclude, average sap flow rate of trees subjected to R treatment was lower compared to trees in C treatment by 17 % in 2013, 33 % in 2014 and 41 % in 2015. Note, that this calculation does not consider the tree S1.

5.3.2.1 Scaling sap flow to stand level

Transpiration estimates of sap flow from a sample of individual stems (kilograms or liters) must be scaled to an area basis (mm of water column per m²) for reasonable interpretation, thus allowing for comparison with other components of water balance. To quantify water use in forests, several methods are available for assessing spatial and temporal variations in water use, which are based on combining sap flux and sapwood area of all trees within an area of interest. To translate volume-based estimates of transpiration to depth units, a conversion that recognizes the area occupied by the trees is required. In tree plantations with trees of the same size and regular spacing (such as short rotation coppice plantation) with very few gaps in the canopies, the area occupied by a given tree (its domain) with respect to its contribution to the total transpired flux from the site may be reasonably approximated (Vertessy et al., 1995). Thus, the sap flux densities measured by three sensors per each experimental plot were averaged and multiplied by total cross sectional area of conductive xylem of all trees within particular plot. This procedure worked well for 5 of 6 experimental plots, with exception of R treatment at block 3. The dominant tree S1 exhibited exceptionally high sap flux density rates, which exceed two times the sap flux density of other trees within this experiment. Nevertheless, the S1 was included in scaling, what increased estimation of transpiration from R treatment of block 3.

5.3.3 Transpiration

Transpiration was calculated combining sap flux data and respective cross sectional area of all trees and shoots within each experimental plot (throughfall exclusion and control treatment) and replication (block 1, 2, 3) in four consecutive growing seasons 2012–2015. Within this thesis the growing season is considered as a period between April and November. From phenological point of view, the average length of growing season (daily mean air temperature above 5°C) at the experimental site Domanínek represents 217 day (calculated from long term average 1981–2010). According to phenological observations from phenocameras installed at the plantation it was estimated, that bud burst occurs each year as soon as the sum of days with mean air temperature $\geq 5^{\circ}\text{C}$ measured from the beginning of the year reaches $\sim 100^{\circ}\text{C}$. This happens usually around 3rd week of April. The empirical agreement between 100 °C threshold and bud burst day was considerable stable in years 2012–2015, so it was used for determination of bud burst date in years, when no phenocamera, sap flow nor

personal observations of bud burst were available. The earliest bud burst occurred in 2014 (April 17th), the latest in 2012 (April 29th), the remaining bud burst dates ranged in between. The end of each growing season was determined according to attenuation of sap flow signal together with visual evaluation of remaining foliage. Interestingly, despite the different bud burst days and seasonal climate development in years 2012–2015, the foliage lasted 172 ± 2 days in each year, which represents very little variation. So even though the length of growing season allows growth for typically 217 days, the actual duration of foliage is limited to only 172 days at this site. In other words, 45 days of typical growing season are not used for growth, although it could be. This behavior might be a genetic trait of this hybrid poplar clone.

Once the buds burst took place, the stand transpiration rapidly increases in proportion to the developing leaf area (LAI). The major increase in transpiration is linked with increasing leaf area index from 0 to 3, which happens approximately 2 weeks after the bud burst. Higher air temperature speeds up this process. Moreover, low LAI values (0–2) are more important for transpiration than higher LAI values (4–6). The reason is a non-linear relationship between LAI and the sunlight penetrating down the canopy (Fischer et al., 2013a). In order to calculate the transpiration during the whole growing season, the transpiration occurring prior the start of the sap flow measurement had to be estimated. To deal with this issue an assumption that the transpiration is the function of leaf area was adopted (Fischer, 2012). It was observed, that during periods of LAI above 5 and non-limiting soil water availability, the transpiration rates were similar to the ET_0 . For the rough estimation of the spring transpiration, the transpiration of each treatment and block was linearly interpolated backwards according to the linear relationship between the course of ET_0 and transpiration 10 day after the instrumental measurements started. This relationship was used to interpolate the transpiration backward to the day when bud burst occurred. In the next step the transpiration was linearly decreased from 95 % to 0 % according to the development of LAI from 4 to 0.

In 2012, the phenological growing season started on April 29th, when bud burst occurred and leaf area index development started. The foliage same as sap flux measurements lasted until October 20th. Precipitation totals over the entire year 2012 amounted 511 mm, whereas reference evapotranspiration ET_0 reached 658 mm. Annual ET_0 to P ratio was 1.35, i.e. higher evaporative demand of atmosphere compared to

incoming precipitation. Average air temperature was 7.41 °C. Moreover, the R treatments were dug around with 0.5 m deep trenches insulated with geofoil, in order to prevent entering water from surrounding soil into the treatments and also to prevent roots to grow outside the R treatments.

During the period of ongoing transpiration, the mean ET_o was 2.86 mm d⁻¹ and total reached 522 mm. On Fig. 21 there is depicted daily transpiration amounts of throughfall exclusion treatment (R) and control (C) in particular blocks 1, 2 and 3. The highest transpiration rates are apparent at C of block 1 with seasonal daily average of 2.68 mm d⁻¹, daily maximum 7.25 mm d⁻¹ and seasonal total of 475 mm, representing 91 % of ET_o . The adjacent R plot, subjected to 40 % throughfall exclusion treatment resulted in seasonal daily average of 1.46 mm d⁻¹, daily maximum 4.90 mm d⁻¹ and seasonal total of 259 mm, which is 50 % of ET_o in the given period.

Transpiration at block 2 was slightly higher at R treatment, with daily average 2.56 mm d⁻¹, daily maximum 7.54 mm d⁻¹ with seasonal total of 460 mm, whereas the control treatment reached average daily transpiration 2.36 mm d⁻¹, daily maximum 7.00 mm d⁻¹ with seasonal total 424 mm. This represents 81 % of ET_o for C and 88 % of ET_o for R. Block 3 attained the lowest transpiration rates in year 2012 with daily average of C of 2.17 mm d⁻¹, daily maximum 4.86 mm d⁻¹, whereas daily average of R was 1.88 mm d⁻¹, daily maximum 4.81 mm d⁻¹. This resulted in seasonal totals of 390 mm and 75 % of ET_o for C and 337 mm and 65 % of ET_o for the R treatment. To conclude year 2012, average daily transpiration of C treatments across all blocks reached 2.40 mm d⁻¹, whereas transpiration of R treatments across all blocks was 1.97 mm d⁻¹. Seasonal total for C treatment was 430 mm, representing 82 % of ET_o , whereas for R treatment the seasonal total reached 351 mm, representing 75 % of ET_o . In other words, precipitation income decreased by 40 % resulted in 78 mm lower transpiration total representing 18 % decrease compared to control treatment. Note that transpiration estimates of year 2012 were based on measurements of 8 sensors distributed across 6 experimental plots (C and R treatment in three blocks). From that reason this results are less robust than transpiration estimates calculated in following years when 18 sensors was installed and used for scaling. Thus, year 2012 was left out from further comparison of transpiration from years 2013–2015.

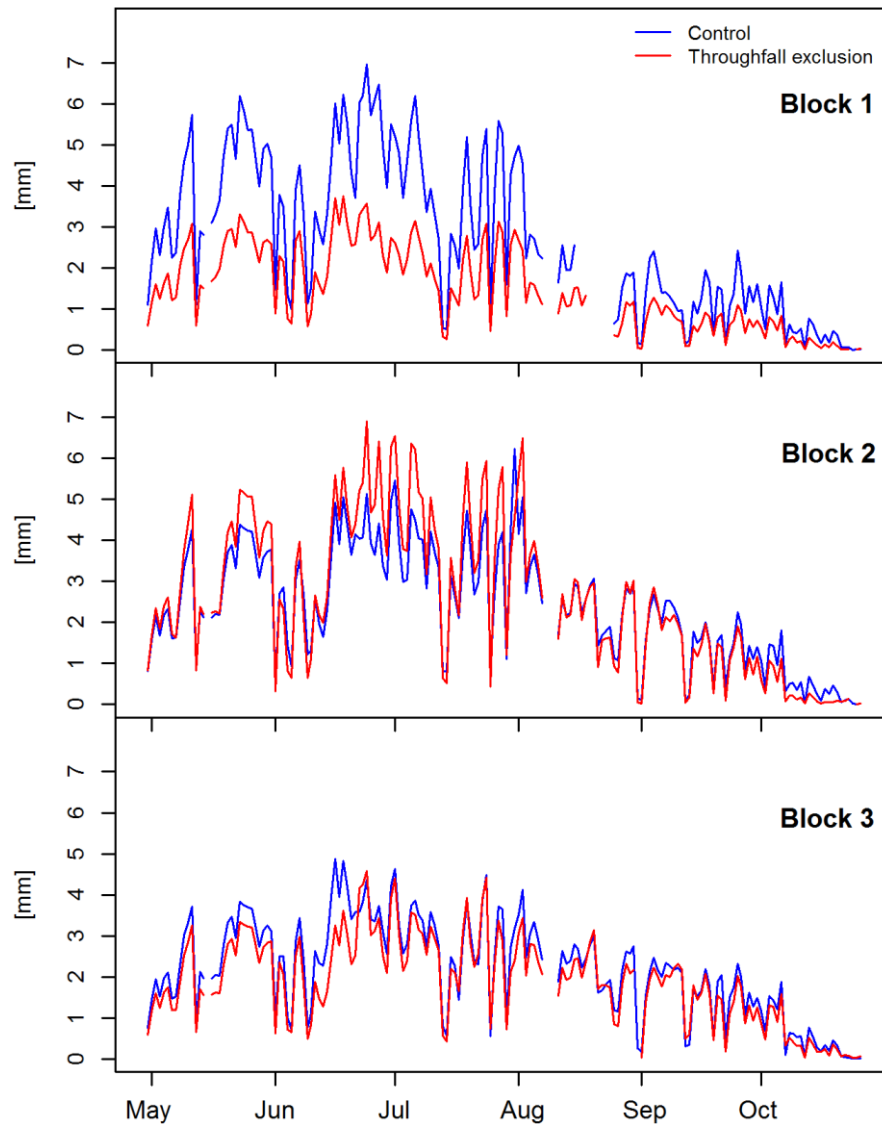


Figure 21: *Daily transpiration (mm) of control and throughfall exclusion treatment in blocks 1, 2 and 3, during growing season 2012.*

In 2013, the bud burst occurred on April 25th. The leaf area developed until it reached its peak value 8.2 on July 23rd. Loss of the foliage together with cease of sap flow signal occurred on October 12th. In mid June 2013 the throughfall exclusion was raised from 40 to 70 % by installing additional plastic roofs. Annual precipitation totals over year 2013 amounted 529 mm, whereas reference evapotranspiration ET_0 reached 607 mm. ET_0 to P ratio was 1.2 and average air temperature was 7.3 °C. During the period of ongoing transpiration the average daily ET_0 was 2.88 mm d⁻¹ and the total amount was 492 mm.

On Fig. 22 are shown daily transpiration rates of all treatments and blocks during growing season 2013. Similarly as in year 2012 the highest transpiration rates are apparent at C of Block 1 with seasonal daily average of 2.95 mm d^{-1} , daily maximum 6.99 mm d^{-1} and seasonal total of 495 mm, representing 101 % of ET_0 . The neighboring R plot, subjected to 70 % throughfall exclusion treatment resulted in seasonal daily average of 1.85 mm d^{-1} , daily maximum 5.38 mm d^{-1} and seasonal total of 310 mm, which accounts for 63 % of ET_0 in the given period.

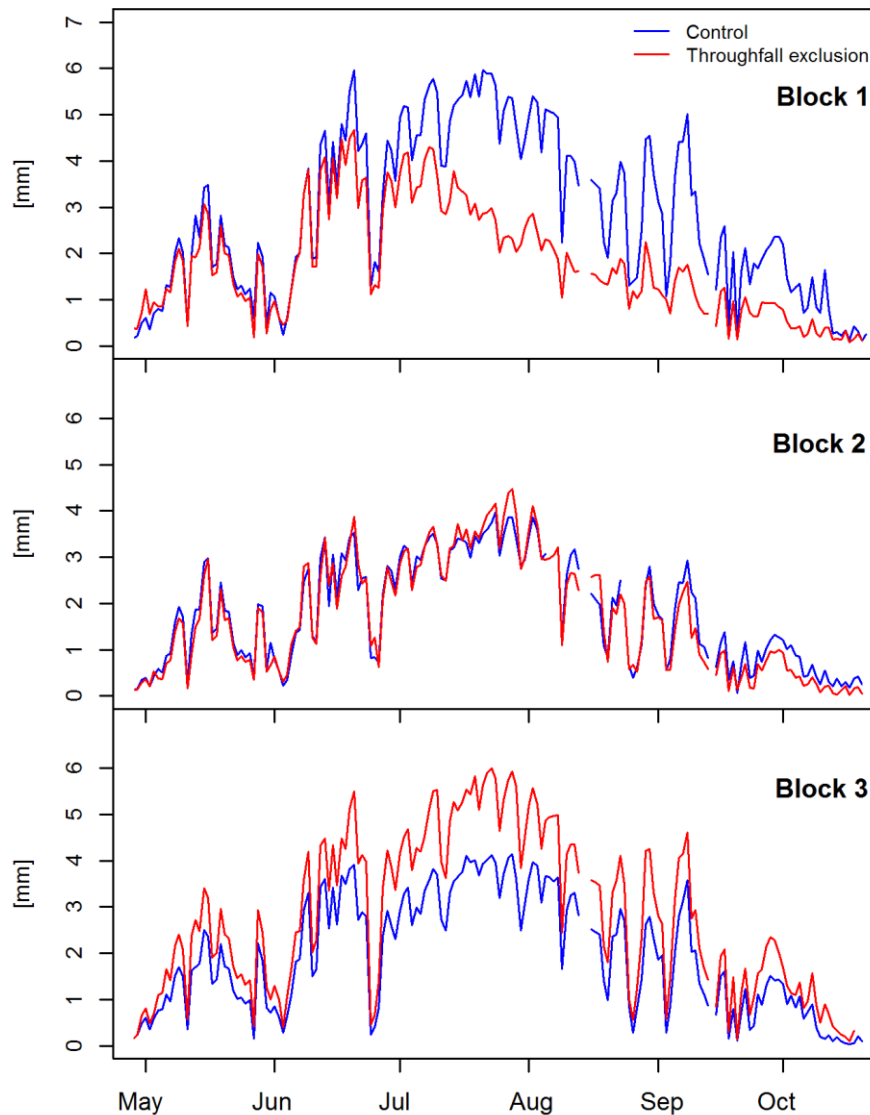


Fig. 22: Daily transpiration (mm) of control and throughfall exclusion treatment in blocks 1, 2 and 3, during growing season 2013.

Transpiration of C treatment at block 2 prevailed this year with daily average 1.89 mm d^{-1} , daily maximum 5.08 mm d^{-1} with seasonal total of 310 mm, while the R

treatment reached average daily transpiration 1.79 mm d^{-1} , daily maximum 5.15 mm d^{-1} with seasonal total 300 mm. This represents 63 % of ET_o for C and 61 % of ET_o for R. Since 2013 the transpiration estimates at block 3 performed opposite pattern, than expected, i.e. transpiration estimates of control treatment were lower than transpiration of R treatment. This effect was caused by exceptionally high rates of sap flux density, observed at single dominant tree with code S1 in the middle of R treatment at block 3, which outweighed the resulting transpiration calculation upwards. The high sap flow rates of tree S1 can be seen on Tab. 9 in section with results of sap flow measurements. Thus, the daily average transpiration rates in year 2013 of C reached 2.04 mm d^{-1} with daily maximum 4.54 mm d^{-1} , whereas at R treatment it reached 2.89 mm d^{-1} with maximum 5.99 mm d^{-1} . This resulted in seasonal totals of 342 mm and 69 % of ET_o for C and 484 mm and 98 % of ET_o for the R treatment. Generally, during growing season 2013 the average daily transpiration of C treatments of all blocks reached 2.29 mm d^{-1} , whereas transpiration of R treatments was 2.18 mm d^{-1} . Seasonal total for C treatment was 382 mm, representing 78 % of ET_o , whereas for R treatment the seasonal total reached 365 mm, representing 74 % of ET_o . Thus, in this season the precipitation income decreased by 70 % resulted in 17 mm lower transpiration total representing 4 % decrease compared to control treatment.

Daily course of transpiration of C and R treatment at block 1 and ET_o shown at Fig. 23 illustrates the typical scenario after major precipitation event (47.5 mm on June 28th 2013). First 8 days after the rain the transpiration rate of both C and R treatment matches the rate of ET_o . Despite the throughfall exclusion treatment, which drain 70 % of throughfall away, there is still 30 % available, representing 14.3 mm of water entering the R plot. Trees are taking advantage of this surplus water and transpiration of both treatments matches the ET_o . During the next 10 days of high evaporative demand the transpiration slowly declines as trees deplete the soil water reservoir refilled by the foregone rainfall. This decline is more pronounced at R treatment. During last 10 days (July 19th–July 28th) the decline in transpiration of both treatments steadily continues, but the pace of declining at R treatment is much faster. In addition, the shape of the diurnal transpiration curves of R treatment shows characteristic pattern with the peak transpiration occurring before noon (usually between 9:30 to 11:30) and subsequent decline, what indicates water stress and reducing of the stomatal aperture.

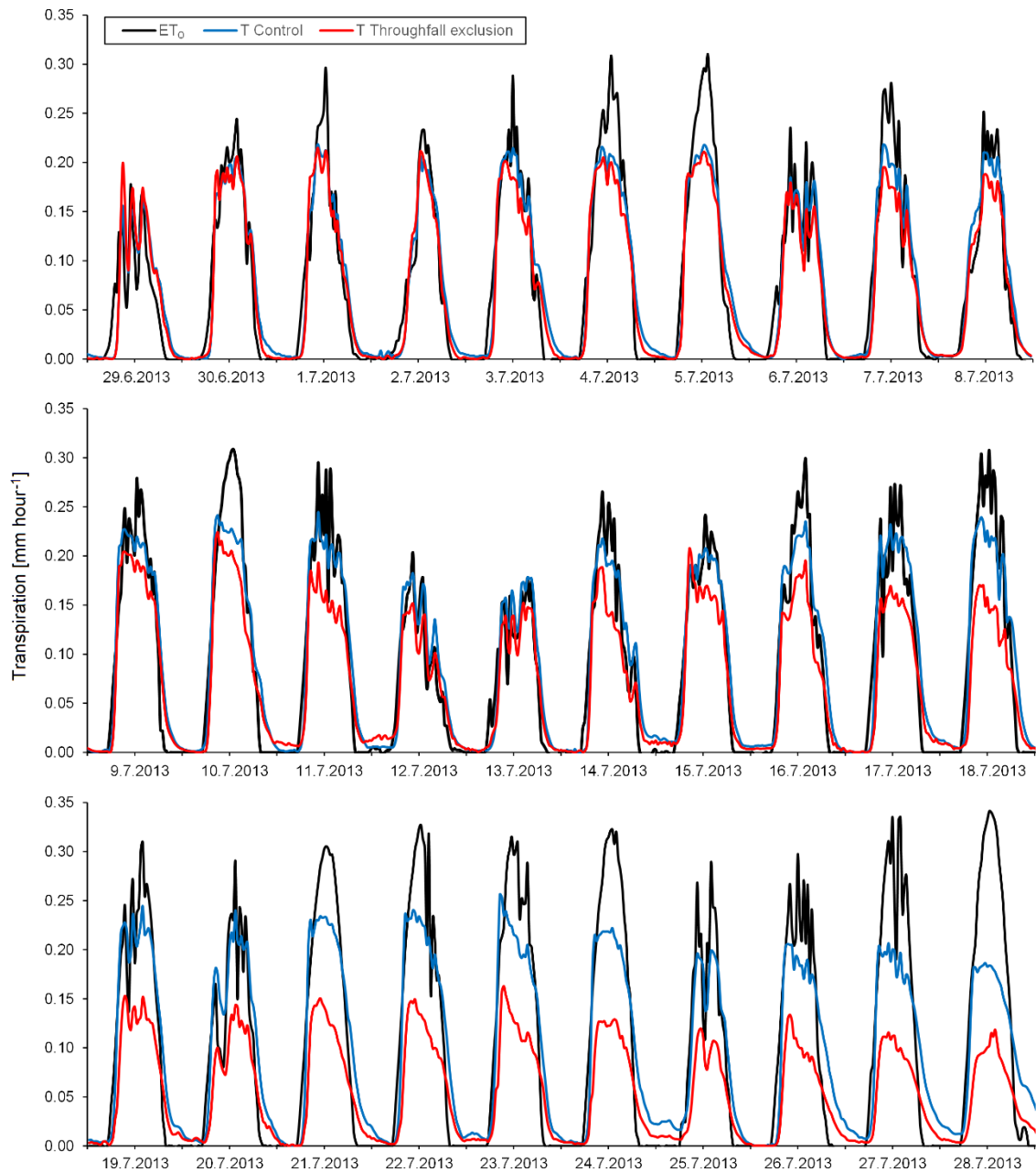


Fig. 23: Diurnal courses of ET_0 , transpiration of control (C) and throughfall exclusion treatment (R) shows 30 days without rain following after an abundant rainfall (47.5 mm on June 28th 2013). Note, that shortly after rain the ET_0 , C and R have similar magnitude. As the time proceeds, transpiration of C and especially R (receiving 70 % less throughfall precipitation) water declines.

Daily average transpiration rates in year 2014 are depicted in Fig. 24. The bud burst occurred on April 17th, the peak LAI of 7.5 was reached on August 19th and trees shed leaves on October 6th. Average air temperature was 8.78 °C, annual precipitation was

559 mm and the annual total of ET_o reached 581 mm, i.e. ET/P ratio of 1.04. The average daily transpiration rates of C treatment at block 1 reached 2.21 mm d^{-1} , daily maximum of 6.21 mm d^{-1} with seasonal total 378 mm, i.e. 80 % of ET_o . Contrarily, the R treatment at the same block maintained average daily transpiration of 1.18 mm d^{-1} , daily maximum 5.04 mm d^{-1} with seasonal total of 202 mm, which is 43 % of ET_o . Block 2 showed higher transpiration rates compared to previous year with daily average of C reaching 2.32 mm d^{-1} , daily maximum 5.54 mm d^{-1} and seasonal total 395 mm, which is 84 % of ET_o . On the other hand, the R treatment had lower average daily transpiration 1.95 mm d^{-1} , daily maximum 5.25 mm d^{-1} and 334 mm annually, resulting in 71 % of ET_o . The average daily transpiration of C reached only 1.59 mm d^{-1} , daily maximum 5.37 mm d^{-1} , whereas at R treatment it reached 2.37 mm d^{-1} with peak daily transpiration of 5.85 mm d^{-1} . This resulted in seasonal totals of 272 mm and 58 % of ET_o for C and 404 mm and 86 % of ET_o for the R treatment. If we compare transpiration of both C and R treatments in 2014, then the C treatment had average daily transpiration 2.04 mm d^{-1} and seasonal total 348 mm, which is 74 % of ET_o , whereas R treatment showed lower daily average 1.83 mm d^{-1} and seasonal total 313 mm. Transpiration of R treatments was lower by 35 mm, which represents 10 % decrease compared to transpiration of controls.

In the year 2015, the average air temperature was $8.68 \text{ }^\circ\text{C}$, precipitation amounted only 416 mm and ET_o reached 657 mm, which represents ET/P ratio 1.58. Average daily transpiration of C treatment at block 1 reached 2.63 mm d^{-1} , with daily maximum 6.99 mm d^{-1} , whereas R transpired only 1.31 mm d^{-1} , daily maximum 5.60 mm d^{-1} . Seasonal totals for C and R reached 456 mm and 228 mm, which is 85 % and 42 % of ET_o , respectively. The C treatment at block 2 showed average daily transpiration 2.20 mm d^{-1} , daily maximum 5.69 mm d^{-1} , whereas the R treatment transpired only 1.87 mm d^{-1} , but with the maximum daily transpiration of 7.64 mm d^{-1} , which the highest daily transpiration observed during this study. Seasonal totals for C amounted 381 mm and for R treatment 323 mm, which represents 71 % and 60 % of seasonal total ET_o . Transpiration at block 3 maintained the same reverse pattern as in years 2013 and 2014. Average daily transpiration of C and R treatment reached 1.21 mm d^{-1} with maximum 3.41 mm d^{-1} and 2.58 mm d^{-1} with maximum 6.28 mm d^{-1} . Seasonal total for C and R treatments reached 208 mm and 448 mm, resulting in 39 % and 84 % of the seasonal ET_o .

To conclude, in 2015 the mean daily transpiration of C treatments was 2.01 mm d^{-1} and R treatments 1.92 mm d^{-1} , which represents seasonal total of 348 mm and 333 mm for C and R respectively. The decrease in transpiration of R treatment was 15 mm, representing 4 % less, than transpiration of C treatments. Moreover, compared to 2014, the daily course of transpiration shows two seasonal maxima of transpiration - the first in late May and June. Then followed continuous decrease in transpiration caused by the severe drought. After a storm event with heavy rain on August 18th 2015 (82 mm in 28 hours) a second peak of transpiration followed and higher transpiration was maintained until mid-September.

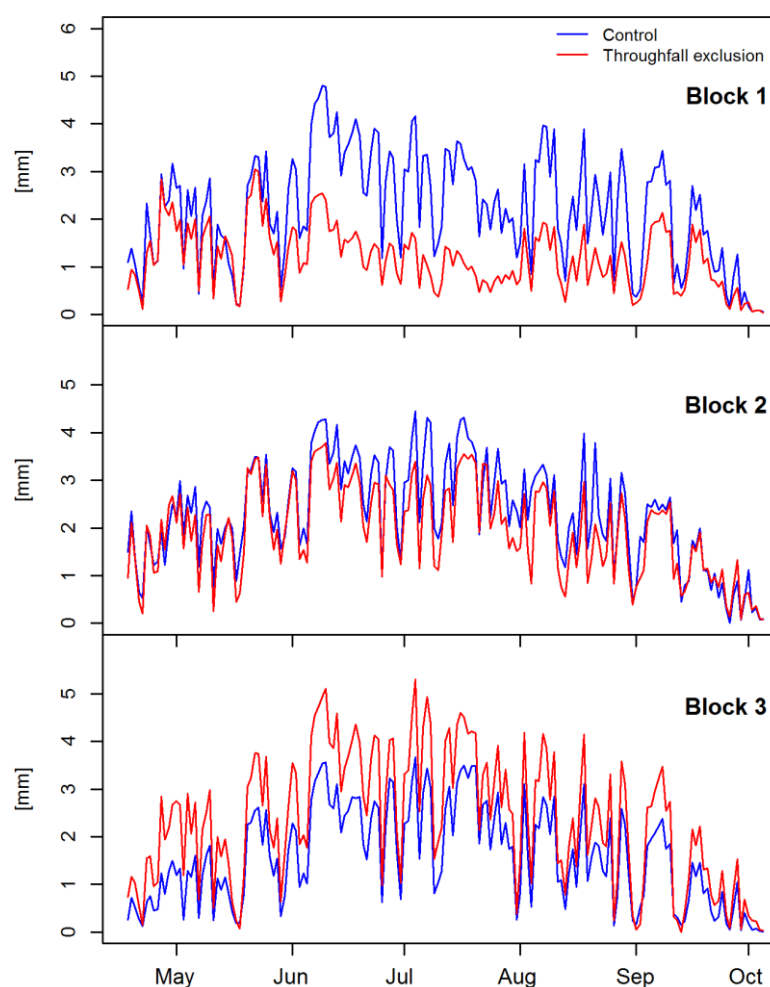


Figure 24: *Daily transpiration ($\text{mm/m}^2/\text{day}$) of control and throughfall exclusion treatment in blocks 1, 2 and 3, during growing season 2014.*

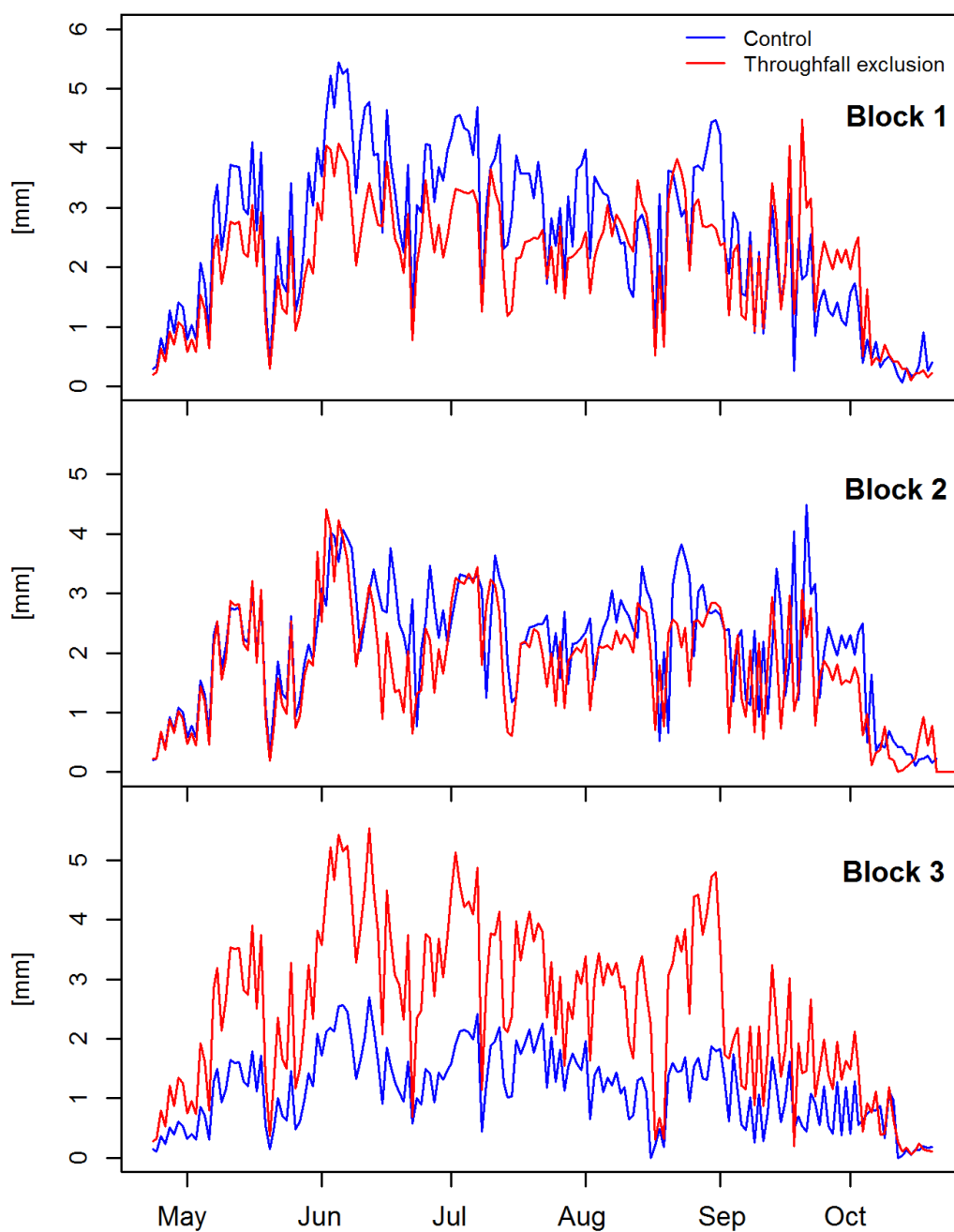


Figure 25: *Daily transpiration (mm/m²/day) of control and throughfall exclusion treatment in blocks 1, 2 and 3, during growing season 2015.*

At the seasonal level (averaged growing seasons 2012–2015) the transpiration of C treatment represented 75 % of ET_0 whereas transpiration of R treatment represented 68 % of ET_0 during average growing seasons. Mean daily transpiration of C reached 2.19 mm d^{-1} , whereas mean daily transpiration of R was 1.98 mm d^{-1} . To provide more

detailed comparison on monthly scale, Fig. 27 depicts boxplot with transpiration of C and R treatment during growing seasons 2013–2015. It can be seen, that highest transpiration in 2013 occurred in July and the transpiration rate distribution resembles a Gauss curve. In April to June the transpiration of R treatments prevails, but since July it declines, as the water scarcity at R treatments limits transpiration through stomata aperture. In the beginning of 2014 there can be seen similar trend, as in previous year, but the median daily transpiration of C starts to be higher than R since June, although the monthly peaks of transpiration are higher at R treatment. This suggests forthcoming throughfall exclusion effect. In addition, in 2014 absolute values of transpiration of C and R are lower, compared to year 2013 as a result of dry spring which prevented high transpiration rates during peak summer period at both treatments. The maximum transpiration rates are shifted from July to June. In 2015 higher transpiration of C treatment becomes apparent since May and remains so until September. Fig. 26 shows boxplots with comparison of C and R, where seasonal transpiration of individual blocks are pooled in years 2012–2015. Daily median transpiration is higher at C, but maximum values 2013–2015 are associated with R treatment. Seasonal comparison of C and R treatment on individual block level is depicted on Fig. 28. There can be seen an apparent variability among treatments. In 2012 and 2013 the throughfall exclusion effect was not so pronounced as in 2014 and 2015.

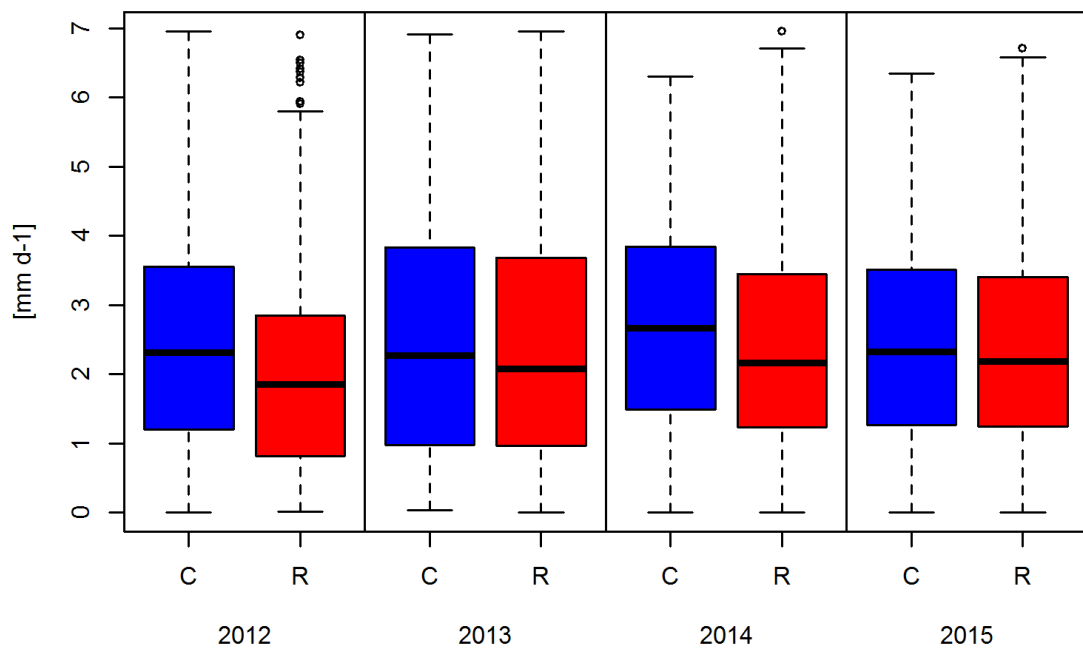


Figure 26: Comparison of daily transpiration rates of control and throughfall exclusion treatment during growing seasons 2012–2015.

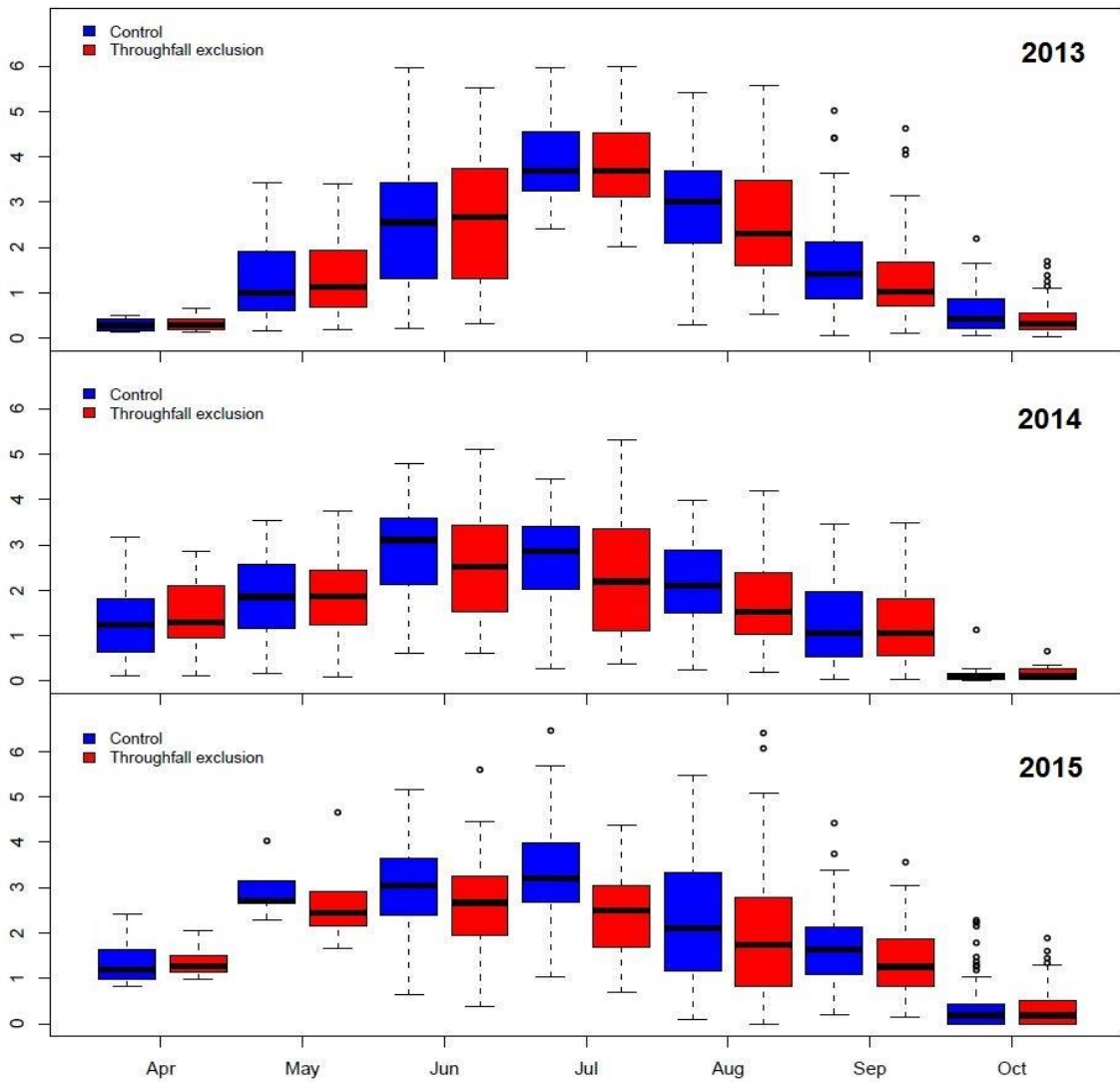


Figure 27: Daily transpiration (mm) of control and throughfall exclusion treatment on monthly basis during growing seasons 2013–2015.

Table 10: Seasonal totals of precipitation, ET_o and transpiration at particular treatment and block.

		Seasonal total (mm)				
	Treatment	Block	2012	2013	2014	2015
Transpiration	C	1	476	495	378	456
	R		259	311	202	228
	C	2	424	310	395	381
	R		460	301	334	323
	C	3	390	342	272	208
	R		337	484	404	448
Precipitation			298	347	385	246
ET_o			522	492	471	537

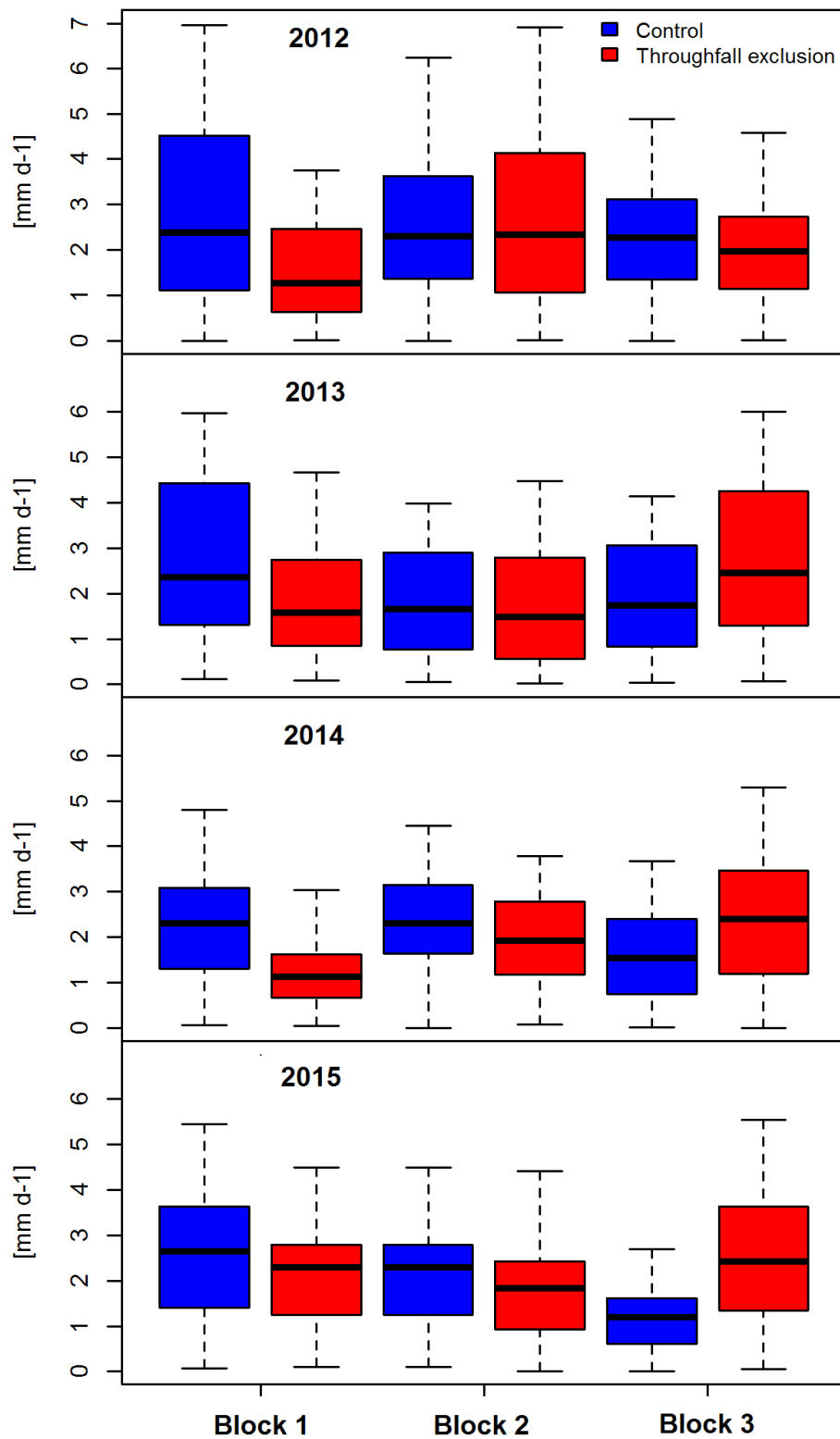


Figure 28: Comparison of seasonal transpiration rates (mm d^{-1}) of control and throughfall exclusion treatments in particular blocks in 2012–2015.

5.3.4 Water use efficiency

In 2011 the average water use efficiency on tree level reached 3.38 g kg⁻¹ over period August-September. In years 2012–2015 the WUE was calculated as a product of seasonal transpiration total and annual above-ground biomass productivity per particular plot and resulted in 3.17 and 3.00 g kg⁻¹ for C and R, respectively. In 2012 the seasonal WUE of C and R reached 3.07 and 3.51 g kg⁻¹, respectively. In 2013 WUE increased for C to 3.69 g kg⁻¹ and R decreased to 3.25 g kg⁻¹. In 2014 the WUE further increased to 3.85 g kg⁻¹ for C and 3.82 g kg⁻¹ for R. Year 2015 was the driest compared to previous years and the water shortage drove WUE of C to 4.23 and WUE of R decreased to 3.58 g kg⁻¹. Fig. 29 depicts how decreased soil moisture level at particular plot influences WUE. Note, that block 2 was omitted from this comparison, as block 2 showed good soil water availability at both treatment. Thus, the effect of soil moisture on WUE was not present.

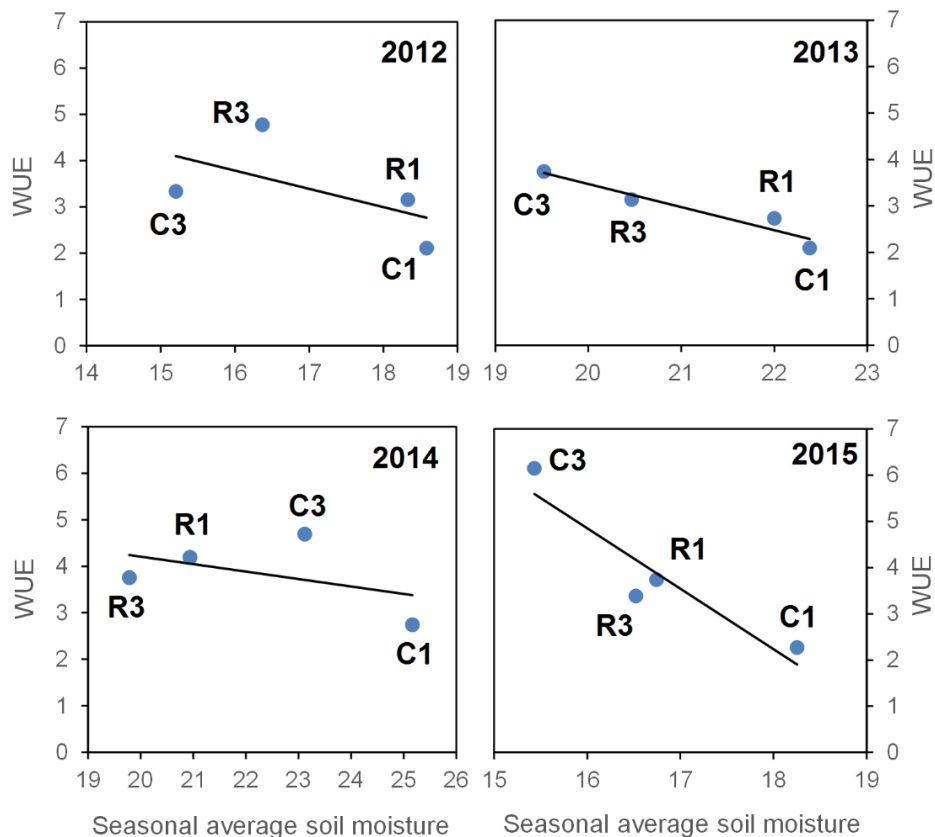


Figure 29: Relationships between water-use efficiency and average seasonal soil moisture at particular C and R treatment of block 1 and block 3. There can be seen how decreasing soil moisture enhances water-use efficiency.

5.4 Discussion

5.4.1.1 Determination of maximum temperature difference

Estimation of sap flux density by the heat dissipation method relies on measurement of a single parameter, i.e. daily fluctuation of the temperature difference (ΔT) between heated and unheated probes. Apart from the monitored water movement, the daily course of the temperature difference between upper and lower thermocouple is affected by the xylem thermal properties, which is linked to its water content and the current applied to the heating element of the probe (Clearwater et al., 1999; James et al., 2002; Oliveras a Llorens, 2001). Daily maximum temperature difference (ΔT_{\max}) is a critical parameter for calculation of sap flux density using heat dissipation method (Lu et al., 2004). Basically, ΔT_{\max} occurs when $F_d = 0$, i.e. no water flowing through the conductive xylem. This situation occurs usually between midnight and dawn, when VPD is close to zero. As a result of absence of atmospheric evaporative demand, the transpiration ceases overnight and the tree internal water storage refills after being depleted during midday period of high transpiration rate. Because there is no movement of water, which would otherwise absorb and transport the heat upwards through the stem, the measured ΔT is reaching constant value. Many factors may prevent the occurrence of the zero flow state, such as night-time water movement for new growth (vegetative or reproductive), slow restoration of tree's internal water storage during prolonged drought and water loss from the canopy due to high vapor pressure deficit and high wind speed (Snyder et al., 2003). Abovementioned night-time water flow affects the determination of the sap flow by underestimating the real ΔT_{\max} , which is necessary for calculation of F_d , which results in underestimation of F_d . The parameter ΔT_{\max} is not stable over time. Drift in ΔT_{\max} is mainly influenced by the thermal properties of the wood surrounding the heated probe, when ΔT_{\max} of dry wood is usually higher than for wet wood. Daily values of ΔT_{\max} tend to shift by the order of several degrees Celsius during the development of a severe soil water deficit. Such drift occurs during both drying and re-wetting phases (Lu et al., 2004).

Parameter ΔT_{\max} should be determined for each sensor separately, as ΔT_{\max} is probe/measurement point specific. There are several ways to determine ΔT_{\max} . Firstly, it can be determined visually based on empirical observation of ΔT and meteorological variables, such as VPD and precipitation. The person processing the dataset observes

the course of ΔT and combinations of other driving variables, such as solar radiation, VPD, soil moisture and precipitation events. Based on combination of these variables the evaluator judges which day was the ΔT_{\max} represented the no-flow conditions or not. This approach is not straightforward in case of processing more channels measuring over longer time period. It requires experience, it is time consuming and there is no guarantee, that each signal is processed exactly in the same way. From that reason, unified approach ΔT_{\max} determination was developed, in order to determine the ΔT_{\max} of all sensors in the same way.

5.4.1.2 Sap flux density

Within this study sap flux densities (F_d) were calculated applying the Granier equation with the original empirically-derived parameters (Granier, 1985). A number of studies have shown, that the original empirical parameters of the Granier equation are suitable for diffuse porous trees (Granier et al., 1996; Smith a Allen, 1996; Steppe et al., 2010; Vandegehuchte a Steppe, 2013), including poplar (Bush et al., 2010). However, an important potential limitation of this technique is that the empirical calibration has little physical basis (Clearwater et al., 1999; Smith a Allen, 1996). Within this study a wide range of sap flux densities from 10 to 121 $\text{cm}^3 \text{m}^{-2} \text{s}^{-1}$ were observed at sampled trees in the same day. This was partly caused by the effect of the throughfall exclusion and thus decreased soil water availability at R treatments and partly by natural heterogeneity of the stand, which was result of competitive growth relationship among vast number of shoots re-sprouted after the first harvest of the plantation in 2009. Oren et al. (1998a, 1998b) reported that the tree-to-tree variability in terms of F_d can result from competition and exposure to the atmosphere depending on the canopy positions of individuals. As well, individuals with a higher stem density can have low sap flux density and individuals with a lower stem density can have a higher sap flux density. The median F_d at R treatments was lower compared to controls in every growing season, with an average decrease of 21.1 % for period 2011–2015. Schwendenmann et al. (2010) performed an 80 % throughfall exclusion experiment at cacao plantation in Indonesia with experimental design similar to this study. Despite the decreased soil water content down to a depth of 2.5 m, contrary to expectations they measured only relatively small (11 – 12 %) decrease in sap flux densities of cacao and *Gliricidia* in R treatment.

5.4.1.3 Gap filling

Gap filling treatment was necessary for every year of sap flow measurements. If we consider the probe design comprising of 2 thermocouple wires and 2 wires for the heating element, all of them of 0.05 mm diameter while exposed to the harsh natural environment for the entire growing season, the occasional sensor failure was inevitable. In addition, the source of constant current for the sensor heating elements required serial connection of heating elements. Thus, the heating elements of 4 sensors were hooked up on a single wire. If any damage occur to this constant current supply wire, whole group of 4 sensor is non-functioning. The most frequent reason of sensor failure is water leakage, rust and mechanical disturbance. Gap filling was needed especially for dataset from growing season 2013. The reason was change in measurement setup, when three V16 datalogger (EMSBrno, Brno, Czech Republic), which were used in previous growing seasons were replaced by three aged Campbell CR10 dataloggers (Campbell Scientific, Shepshed, UK). These DL's are not equipped with back up batteries, which could hold DL settings and memory when DL is disconnected from power. Any loss of supply voltage led to loss of measurement record and DL reset. This situation accidentally happened several times due to external forcing (wind, wildlife) or during changing batteries. In addition, one CR10 connected to six sap flow gages at Block 2 was not able to start measurement several hours (sometimes several days) after the 12 V DC supply battery was replaced with a re-charged one. Despite some measures applied (e.g. backup 12 V DC battery bridge, where CR10 was connected while replacing the main battery), loss of data occurred time to time. Unlike other CR10s installed at Block 1 and 3, where single sensor failure occurred while remaining sensor were measuring correctly, the CR10 at Block 2 was either running, or shut down, i.e. all sensors were involved. Thus sap flux velocity data of all 18 sensors from three DL CR10 working on Blocks 1 - 3 were pooled together. The Gap filling software worked well and was able to fill all gaps if at least one sensor was measuring.

5.4.1.4 Sapwood area determination

Determination of sapwood is crucial procedure when calculating sap flow. The heat dissipation method provides solely an information about sap flux density, i.e. the actual flux of sap ascending through hypothetical cross sectional area of tree sapwood. The original Granier equation states, that the total sap flow in a tree is a function of the sap

flux density and the sapwood cross-sectional area (Granier, 1987). Sap flow in whole trees is typically measured over a relatively narrow range of sapwood depth, usually close to the vascular cambium in new xylem where sap flux density is typically the highest (James et al., 2002; Lu et al., 2004). If sap velocity diminishes rapidly with increasing depth (due to nonfunctional vessels), large errors in estimates of whole-tree mass flow can result when sap flux density is multiplied by sapwood area (Čermák a Nadezhdina, 1998; Meinzer et al., 2001; Wullschleger a King, 2000). Previous studies have shown that radial variation in sap velocity clearly exists in many woody species (Čermák et al., 1992; Dye et al., 1991; Gebauer et al., 2008; Phillips et al., 1996; Wullschleger a King, 2000), with sap velocities being greatest in outer sapwood and significantly lower with increasing proximity to heartwood. Studies that do recognize radial variation as an important consideration in extrapolating sap velocity to the canopy scale, often use only limited measurements (one to two trees) to quantify this parameter (Smith a Allen, 1996; Wullschleger a King, 2000). From that reason a special attention was given to the problem of sapwood determination. Several methods were tested. Firstly, applying dye solution (i.e. eosin dye) into a predrilled hole in the tree trunk (Čermák et al., 1992; Gebauer et al., 2008). After couple of hours the tree was cut down a further split into 10 cm long segments and traces of dye were investigated. Secondly, cutting the tree “under water” and placing the cut tree into a bucket with a dye solution. Ascent of sap sucks colored solution up the sapwood. The tree was processed similarly as in previous attempt. However, it was not possible to obtain an accurate and generally valid parameter, fully characterizing the portion of sapwood in cross sectional area among different trees and during time. Poplar belongs among tree species with a diffuse porous xylem where the radial sap flux velocity should be uniform (Dickmann et al., 2002; Phillips et al., 1996), which is supported by findings of Gebauer et al. (2008), who reported that the hydro-active sapwood occupied 70 to 90% of the stem cross-sectional area in mature trees of diffuse-porous species. That is why this problem was addressed at this thesis as well. It was assumed, that the best way, how to determine sap flux density in different sapwood depths is measuring sap flux density in outer (0–2 cm) and inner (2–4 cm) ring of the stem cross sectional area. This should also provide an information whether the ratio changes in time, as some studies are based on measurements lasting few days only (Phillips et al., 1996). Sapwood determination experiment revealed, that this ratio is not close to 1, but as low as 0.24. In other words,

the amount of water passing through inner central part of tree stem is only 24 % of the amount passing through the outer diameter. Assuming that whole xylem represent homogeneously conductive sapwood would cause large errors in tree sap flow estimates (Tsuruta et al., 2010). If the sap flux density measured in the outer xylem only is considered as constant towards the center of the tree trunk, then large overestimation of the tree sap flow would be introduced when sap flux density of outer sapwood would be multiplied by the whole tree cross sectional sapwood area. The sap flux density reduction parameter 0.24 can be considered as robust result, because such sap flux density profile ratio was present at all investigated trees with very little variation. As all sap flow measurements presented in this thesis were solely measured in outer sapwood, this result allowed to correct the calculation of sap flow rate for trees thicker than 4 cm in diameter. In this way the sap flow rate of tree with DBH of 4 cm or more was calculated as the sap flux density measured at the outer sapwood (0 – 2 cm) multiplied by the area of outer sapwood, plus sap flux density of outer sapwood, multiplied by reduction parameter 0.24 and by the area of inner sapwood.

5.4.2 Sap flow

Sap flow measurements were established and sap flow rates were calculated, because it allows gathering of detailed and long term information about water uptake of short rotation coppice (SRC) on a tree level. Originally, tree-related sap flow rates were considered as a baseline data for scaling of tree water uptake to the stand level. However, eventually sap flux density data were used for transpiration estimates, instead of sap flow rates.

From scientific point of view the deployment of sap flow measurements also represented another step towards the possibility of partitioning water balance of SRC (Kool et al., 2014; Lawrence et al., 2007; Rothfuss et al., 2010), since the previous research efforts at the Department of Agrosystems and Bioclimatology implemented robust methods for estimating evapotranspiration over the SRC using Bowen ratio energy balance method (Fischer, 2012; Hou et al., 2010; Iritz et al., 2001; Odhiambo a Irmak, 2012) and eddy covariance method (Aubinet et al., 2012; Baldocchi, 2003; Burba, 2013; Goulden et al., 1996; Stannard, 1997). Note that in 2011, when the throughfall exclusion experiment was planned, there was only limited expertise in sap flow measurements with tissue heat balance method (Fischer, 2012) at this department.

There are various methods for estimating tree water uptake (Clausnitzer et al., 2011; Clearwater et al., 1999; Swanson, 1994; Vandegehuchte a Steppe, 2013; Wilson et al., 2001), the most important of them were described in methodology. Each method has its limitation, advantages and shortcomings; in case of this study the critical parameter was minimum and maximum tree diameter, where certain method could be applied. From that point of view young poplar SRC can be a tricky object to measure sap flow due to its fast growth and development (Dickmann et al., 2002). Hybrid poplar rapidly increases stem diameter year to year and there is no method available, which would allow measuring sap flow on trees with DBH of 20 – 120 mm consistently during whole rotation cycle. The studied plantation was harvested in early spring 2009 and the period 2009 – 2013 was associated with rapid increase of stem diameter. From that reason, there were three methods for sap flow measurements, which were tested. Apart from the heat dissipation method (Granier, 1987; Granier et al., 2000; Isarangkool Na Ayutthaya et al., 2010; Lu et al., 2004), sap flow was measured in years 2011–2013 applying stem heat balance method (Čermák et al., 2004; Lindroth et al., 1995) in 2011 and tissue heat balance method in 2012 and 2013. The first sap flow system within this experiment comprised of 8 Granier heat dissipation sensors (UP GmbH, Cottbus, Germany) for monitoring sap flux density of trees with measurement point diameter above 40 mm (dominant shoots) and 4 sensors EMS62 (EMSBrno, Brno, Czech Republic) for monitoring sap flow rates of shoots (or branches) with diameter up to 20 mm. This system was delivered from manufacturer (EMS Brno) on August 4th 2011 and immediately installed at block 1. During August–October 2011 the performance of whole system as well as handling and maintenance was tested. This experiment revealed the mean daily sap flow rate of 4.5 kg per tree, based on 6 sampled trees with DBH 50.9–60.6 mm. This very first attempt of sap flow measurement can be considered as a test of skills and methods and due to its different experimental layout compared to later years it will not be further discussed within this thesis. Overall results of this measurement campaign can be found in Orság a Trnka (2011). In 2012 the sap flow measurements were extended. The single system from year 2011 was de-installed, rearranged and split into three individual systems, in order to cover 3 independent replications (blocks 1, 2 and 3) within the plantation. Sensors EMS62 were withdrawn and returned to EMS Brno, because majority of trees within the stand already exceeded the diameter 20 mm (what is the upper limit for this method). In addition, the sap flow

sensor ensemble was extended with 18 experimental sensors EMS51 based on tissue heat balance method (Čermák et al., 1973; Kučera et al., 1977; Tatarinov et al., 2005). These new and experimental sensors were borrowed from the manufacturer EMS Brno and in year 2012–2013 were tested within this experiment. Because these data were considered as private trial dataset, results are not shown within this thesis. Remaining 8 Granier sensors from previous season were split among measuring systems at blocks 1 (4 sensors, 2 in C treatment and 2 in R treatment), block 2 (1 sensor in C and 1 in R) and block 3 (same as Block 2). However, in 2012 the sap flow measurement made by the heat dissipation method were affected by a mistake in calculation of heating current for heating elements of Granier sensors. The correct heating power applied to a heated probe must be 0.2 W for this method to work correctly. But the system delivered by EMS Brno provided twice as much heating power (0.45 W.) than requested (0.2 W). The heating elements of probes made by UP GmbH have resistance of 37 Ohm instead of expected 20 Ohms. This overheating resulted in shift in measured ΔT approximately by 20 °C upwards with ΔT_{\max} as high as 30 °C. Thus, if the tree internal temperature is ~ 20 °C, than the temperature around the heated probe is higher than 50 °C. This might have caused wounding of the woody tissue surrounding the heated probe, thus distort the heat dissipation from the sensor through the tissue of the tree trunk (Tatarinov et al., 2005). Nevertheless, this season provided some usable data, which were utilized for analysis of stomatal conductance published in Orság et al. (2012) and Orság et al. (2013b). In addition, these data provided baseline for first transpiration estimates in throughfall exclusion experiment in 2012 (see Fig. 21). Note, that this estimate was performed based on 2 sensors per treatment in block 1 only and 1 sensor per treatment in block 2 and block 3 only. Although the transpiration estimates showed reasonable values, it cannot be considered as robust result, due to variability in sap flow rates among neighboring trees (remember high sap flow rates of the tree S1 in R treatment at block 3). Moreover, drought especially increases the variability in sap flow rates among trees (Köstner et al., 1998). Since year 2013 onwards the methodology was consistent. Sap flow measurements were based on custom-made Granier-type sensors, built according to know-how gained during short term scientific visit at Department of Forestry and Environmental Resources at North Carolina State University (US), where author of this thesis spent almost 2 months in years 2012–2014. This is a common practice at tree physiology laboratories to build heat dissipation sap flow sensors on

their own. The quality, performance and endurance of such sensor is similar to the industrial grade sensor, but the price is at the level of one hundredth of the price of commercially available sensor. Heating elements of such sensor have an average resistance of 20 Ω . In order to achieve heating power of 0.2 W at the heated probe, the supply current must be fixed to 0.10 Amps and the voltage results in 2 Volts. Each experimental block was equipped with 6 such sensors, i.e. 3 sensor in throughfall exclusion treatment and 3 sensors within control plot.

5.4.2.1 Scaling sap flow to stand level

After measuring sap flow, it is necessary to extrapolate water use by sampled plants to an entire stand; mass or volume flow rates for individual plants must be converted to estimates of transpiration per unit area of land (Hatton et al., 1995). There are many sources of possible errors in scaling process, as considerable amount of variation exists at each scaling step encountered (Ford et al., 2007). In uniform stands, such as monoculture crops or forest plantations with closed canopies (i.e. short rotation coppice), the scaling should be relatively simple because most plants in the stand are of similar size and the supply of radiant energy and soil water is uniform (Smith and Allen, 1996). Transpiration is unlikely to vary strongly among the members of such stands, so that sap flow can be measured in a number of individual trees and stand transpiration calculated from tree density (Ham et al., 1990; Smith and Allen, 1996). This approach was adopted for transpiration estimates presented in this thesis. Nevertheless, Hatton et al. (1995) found the greatest potential source of error in scaling from the sensor to tree. To estimate the flux rate of a single Eucalyptus tree (i.e. ring porous tree like poplar) 12 heat pulse sensors were needed to keep the coefficient of variation at 15 %, when sensors were placed randomly, while sample size could be reduced to six when the sensors were stratified by depth a quadrant within the tree (Köstner et al., 1998). Kume et al. (2010) performed a very comprehensive study aimed to assess how sample sizes affect confidence of stand-scale transpiration estimates calculated from sap flux (F_d) and sapwood area measurements of individual trees. He concluded, that for their even-aged, single-species (Japanese cypress plantation) stand in the 20 \times 20 m plot, a sample size of at least 10 sensors for F_d estimates was necessary to account for tree-to-tree variability, but was not necessarily more than 10 trees. The accuracy of transpiration estimates based on these sample sizes with potential errors of 16–21% is reasonable

compared with other methods for estimating water flux such as the eddy covariance technique (Goulden et al., 1996), or the aggregated estimates of evapotranspiration to the landscape scale (Mackay et al., 2002). Čermák et al. (2004) showed that the upscaling error in homogeneous stands sharply decrease with increasing number of sample trees and reaches approximately 15 % and 10 % for 4 and 12 sample trees respectively. In contrast, Petzold et al. (2010) reported that six sample trees in their particular poplar stand were the minimum in order to match a measurement error less than 20 %. Similarly, Cienciala et al. (1999) concluded that with respect to the heterogeneous conditions at the site, the set of 12 trees appeared to be the minimum reasonable sample size to extrapolate tree fluxes into stand transpiration and to monitor simultaneously two tree species. However, in case of this study deployment of 12 sensors per plot was not feasible. It is obvious, that the most accurate approach would be measuring sap flow in all plants within a representative area of land, as was done by Köstner et al. (1992). But it would be hard to achieve it as there is a need for larger number of instruments, such as dataloggers, constant current supply units, batteries and available sample trees. In case of this study, only 6 differential channels were available on datalogger (CR10X, Campbell Scientific, Logan, Utah, US), which were split between 2 treatments (3 + 3). Moreover, there was a limited number of trees suitable for sap flow sensor installation in terms of different DBH and position within each treatment. Finally, majority of suitable trees within treatments had stems already wounded by earlier attempts for measuring sap flow. For example, the proper functioning of the EMS51 experimental sensor required a set of four 1 mm thick plate electrodes to be hammered into the tree stem with radial distance of 90°. These electrodes had to be extracted at the end of each growing season leaving trees injured and more susceptible to disruptive biotic environmental factors (e.g. fungal infection). It is important to realize that sap flow measurements are performed in living organisms, which should be basically unaffected by the method to allow long-term undisturbed observation. Hence, any potential disturbance by excess temperature and tissue damage by sensors and heaters must be minimized to the largest possible extent. Generally said, the measuring arrangement optimal from the technical point of view might be fatal for the measured plant. In practice, only a limited amount of interfering foreign bodies may be inserted into conductive tissues and their size is an extremely important factor too (Tatarinov et al., 2005). Thus, the final sensor ensemble was a tradeoff between number

of sensor required for elimination of errors associated with tree-to-tree differences, number of suitable trees and number of available constant current supply units (for powering sensor heating elements).

5.4.3 Transpiration

Comparison studies of tree stand water use carried out via *in situ* throughfall rain exclusion experiments are quite rare throughout the scientific literature due to high labor demands and difficult interpretation of observed effects, e.g. Hanson et al. (1994). In addition, even less of them is focused on SRC plantations. There is a number of studies quantifying transpiration of SRC under natural conditions i.e. with intact rain water supply (Allen et al., 1999; Hall et al., 1998; Meiresonne et al., 1999; Petzold et al., 2010; Zhang et al., 1999). Some studies compare water use of SRC grown under contrasting water treatments, but mainly in the way of irrigated and non-irrigated treatment (Kim et al., 2008) or combination of non/irrigated and fertilized treatments (Samuelson et al., 2007; Ward et al., 2015). Some studies focused similarly as this one on the effect of throughfall exclusion are performed using trees planted in pots (Souch a Stephens, 1998) or realized in distinctly different climates or ecosystems, such as tropical rain forests (da Costa et al., 2010; Davidson et al., 2004; Davidson et al., 2008; Moser et al., 2014). The most similar study in terms of the experimental layout seems to be the one made by Köhler et al. (2010) and Schwendenmann et al. (2010) who studied responses of sap flux density of 7-year old agroforest subjected to 80 % throughfall exclusion treatment. The 1 ha study stand was subdivided into three throughfall exclusion plots and three control plots and investigated for 2 years. They reported average daily stand transpiration 1.3 mm in throughfall exclusion plots and 1.5 mm in control plots. Despite the decreased soil water content down to a depth of 2.5 m, contrary to expectations they measured only relatively small and changes in sap flux densities.

On the other hand the lack of research studies with similar focus makes results of this thesis unique. The transpiration estimates presented within this thesis are compared with ET_0 , which is used as a reference baseline also in other studies of similar focus. According to modelling study by Persson a Lindroth (1994), the transpiration for a well-established short rotation coppice stand constituted approximately 66 % of total ET on a seasonal basis with relatively small variation between years. This results is related to fertilized and irrigated willow SRC from central Sweden. Similar ratio between

transpiration and ET was reported by Fischer (2012) from neighboring SRC plantation in Domanínek and found transpiration to ET ratio to be 0.7. This is most likely caused by the location of the plantation in downslope in more humid soil with lateral water inflow, which supports higher transpiration rates, compared to SRC plantation of our interest, which is located upslope and subjected to generally drier conditions. This finding is in good agreement with results of this thesis, where seasonal transpiration across growing seasons 2012–2015 constituted 61 % of ET_0 for control treatment and 55 % for throughfall exclusion treatment. Note, that our plantation is not irrigated nor fertilized nor located in humid area, thus the resulting ratio is lower. The T/ET ratio of 0.7 reported also Meiresonne et al. (1999) for hybrid poplar plantation in East Flanders, Belgium, with measurements based on sap flow (heat field deformation method). He also found very similar rates of seasonal transpiration with daily maximum of 5 mm day^{-1} , daily mean 1.9 mm day^{-1} and seasonal total 320 mm. Average seasonal total of control treatment in years 2013–2015 at our site amounted 360 mm. Going south to Viterbo, Italy, Tricker et al. (2009) measured sap flow at *Populus × euramericana* (clone I214) using stem heat-balance method, additionally validated by eddy covariance and reported seasonal daily mean transpiration of 2.66 mm day^{-1} and seasonal maximum 7.20 mm day^{-1} , what are a bit higher values, than those found within this study, but it can be explained by the fact, that the evapotranspirative demand is not balanced by rainfall supply in Mediterranean site conditions (Di Matteo et al., 2015), compared to Bohemian-Moravian highlands. Slightly higher values of mean and maximum transpiration of 3.64 and 4.81 mm day^{-1} , respectively (calculated only for the first week of August 1994) were reported by Hinckley et al. (1994) for hybrid poplar stand in Washington, US. Seasonal daily mean transpiration rate of 2.8 mm for the same clone and sap flow method as presented within this study was reported also by Zalesny Jr et al. (2006) in 2002 in Wisconsin, US. Petzold et al. (2010) described maximum daily rates of transpiration based on sap flow measurements (tissue heat balance) by poplar clone Max 1 (*P. nigra × P. maximowiczii* Henry) in Germany reaching 5.7 and 6.7 mm day^{-1} with seasonal mean (April to September) 2.3 and 2.2 mm day^{-1} in 2007 and 2008 respectively. This is in very well comparable to result from our experiment (the same hybrid clone under very similar climate conditions), where seasonal mean transpiration of control treatments amounted 2.4, 2.3, 2.0 and 2.0 mm day^{-1} for years 2012–2015.

On Fig. 23 there is comparison of daily courses of ET_0 and transpiration of C and R treatments at block 1 in period June 29th – July 28th. This is a good example of the treatment difference, because just prior this period the soil water availability at R treatment was refilled by an abundant rainfall of 47.5 mm on June 28th 2013. Commonly, the growing season starts with saturated soils at both treatments as it has been replenished by winter snowmelt. Subsequently, with the initiation of substantial evaporative demand and canopy transpiration in mid-to-late June the R treatment transpiration is drawn down as the soil water availability at R decreases (Hanson et al., 1998). This happened, when the volumetric soil moisture decreased below ~18 %. Fig. 23 illustrates the abovementioned pattern.

On the other hand courses of ET_0 on Fig. 23 provide a visual evidence, that scaling procedure from tree- to stand-level was performed correctly and the transpiration estimates are robust. When soil water availability is satisfactory and ET_0 moderate the transpiration estimates of both treatments closely match the daily course of ET_0 . However, during the daily peak evaporative demand around noon there can be seen a sharp decrease of transpiration as trees close their stomata to prevent excessive water loss (Bacon, 2009; Dolman et al., 1998; Fitter a Hay, 2001). Similar sharp decline of sap flow in noon was observed also by Fischer (2012), who measured sap flow with tissue heat balance method in the near plantation in 2008 and 2009. Stomatal aperture and the noon decrease in transpiration is more pronounced and sharper at R treatment, due to effective stomatal regulation resulting from decreased soil water availability.

5.4.4 Water use efficiency

In this study the long-term gross WUE was assessed, i.e. ratio between the aboveground woody biomass (stems and branches) and transpired water per unit of projection area. This is considered as a more representative approach, because fluxes of CO_2 and water are integrated over time periods that allow to include respiration losses (Lindroth a Cienciala, 1996). Our results of average WUE of 3.17 (C) and 3.00 $g\ kg^{-1}$ (R) are similar to those reported in literature. Souch a Stephens (1998) reported the WUE of 3.5 $g\ kg^{-1}$ for *Populus deltoides* × *Populus nigra* “Ghoy”. Cienciala et al. (1994) investigated fertilized and irrigated high-density willow stand and they found relatively high values of mean seasonal WUE reaching to 4.1 and 5.5 $g\ kg^{-1}$ for two consecutive years. Our results are also in good agreement to those reported by Fischer (2012), who measured sap flow and stem biomass increments at 3 and 4 mature trees of

the same hybrid poplar clone, planted in the same site, and he reported the seasonal mean WUE to be 3.13 and 3.54 g l⁻¹ in years 2008 and 2009, respectively.

Let's assume, similarly to Lindroth and Cienciala (1996), that an annual production of 10 DMT ha⁻¹ is required to make the short-rotation coppice profitable. Then this amount of production would require seasonal transpiration of 315 mm, based on WUE of C treatment (3.17 g l⁻¹). In previous chapter it was found, that transpiration constituted about 61 % of reference evapotranspiration. Accordingly, 517 mm of water must be available for evaporation to achieve a total annual production of 10 DMT ha⁻¹. Conversely, the average seasonal productivity of control treatment at our study site reached 11.7 DMT ha⁻¹. Given the WUE of 3.17 g kg⁻¹, this requires 369 mm of transpiration, which represents 605 mm of ET_o and that matches the mean annual precipitation of 609.3 mm. However, as seasonal (April–October) precipitation at our site provides only 408 mm (long-term average 1981–2010), remaining water is most likely replenished by winter snow melt and then used in summer during periods of high evaporation demand. During last 7 years of second rotation cycle length the annual ET_o and precipitation at our site amounted 612 and 619 mm, respectively. This suggests, that most of the precipitation water income has been used for evaporation. Thus it can be assumed, as long as the annual precipitation remains above 517 mm, the economical productivity of 10 DMT ha⁻¹ can be achieved.

Moreover, in Fig. 29 there is depicted a linear relationship between average soil moisture and water-use efficiency at particular plot, which means that WUE increases at plots with lower soil water availability, irrespective of treatment applied. The highest WUE 5.05 g kg⁻¹ was associated with treatment with the lowest soil moisture of 15.4 %. Such level of WUE would require only 198 mm of transpiration, 360 mm of ET_o and correspondingly at least 360 mm of precipitation to maintain annual productivity of 10 DMT ha⁻¹. The ability to increase WUE in response to water deficit is necessary feature for drought resistance. In future, it seems to be increasingly important to add traits of drought tolerance and WUE to the panels of criteria already used in poplar selection (Monclus et al., 2006).

5.5 Conclusion

This rain-throughfall exclusion experiment aimed to investigate tree- and stand-water use of an operational poplar-based short rotation coppice (SRC) exposed to expected conditions of future climate, when precipitation water becomes scarcer, while evaporative demand will be higher. Trees grown under 70 % throughfall exclusion treatment (R) showed lower water use compared to control treatment (C) as a result of decreased soil water availability induced by reduced throughfall precipitation. For estimation of tree and stand water use the heat dissipation sap flow method was used. Contrary to expectation, the sap flux density (F_d) was not uniform across whole sapwood cross sectional area. According to measurements of F_d in two depths, inner sapwood ring has only 24 % of F_d measured in outer sapwood ring. Thus, sap flow rates were calculated applying this correction. On the tree level, F_d was lower for trees growing in R. Tree sap flow rates varied according to tree size and social status. Average daily sap flow rates reached 3.6 kg d^{-1} and 2.5 kg d^{-1} in C and R, respectively. On the stand level, transpiration of C and R treatment accounted for 61 and 55 % of reference evapotranspiration (ET_o) during growing seasons 2012–2015. In days with good soil water availability diurnal courses of ET_o and transpiration of C treatment closely matched, indicating, that the sap flux measurement and the scaling procedure were performed correctly. Average daily transpiration reached 2.19 and 1.98 mm d^{-1} for C and R, respectively. Combining transpiration amounts with biomass productivity from previous chapter the water-use efficiency (WUE) of 3.17 and 3.0 g kg^{-1} for C and R, respectively, was determined. Relating WUE of particular plot to seasonal soil moisture average, an inversely proportional linear relationship was found, i.e. trees suffering from water shortage increased their WUE, irrespective of treatment applied. The highest WUE of 5.05 g kg^{-1} was reached at plot with lowest seasonal soil moisture level. Nevertheless, this plot still produced $\sim 5 \text{ DMT ha}^{-1} \text{ yr}^{-1}$. This indicates that poplars are able to increase WUE in response to water deficit and sustain potential severe drought periods in the near future and while still delivering harvestable biomass.

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APENDIXES

Appendix A: List of abbreviations and symbols used in the text

ABP	above-ground biomass productivity
ANOVA	analysis of variance
BREB	Bowen ratio energy balance
C	control treatment
DBH	diameter measured at breast height
DC	direct current
DMC	dry matter content
ET	evapotranspiration
ET _o	reference evapotranspiration
ET _o /P	reference evapotranspiration to precipitation ratio
F _d	sap flux density
HFD	heat field deformation
LAI	leaf area index
PR1	soil moisture profile probe
R	throughfall exclusion treatment
SHB	stem heat balance
S/N	southern to northern
SRC	short rotation coppice
STD	standard deviation
SWP	soil water potential
TD	thermal dissipation
THB	tissue heat balance method
ΔT	temperature difference between upper and lower sensor
ΔT_{max} ,	maximum temperature difference between upper and lower sensor
V	voltage
VPD	vapour pressure deficit
WUE	water use efficiency

Appendix B: List of tables

- Table 1 *Trend analysis of Z Index in particular months during period 1961–2014.*
- Table 2 *Mean air temperature and mean precipitation at experimental site over selected period of time.*
- Table 3 *Monthly course of average air temperature and precipitation totals compared to climatological normal 1961–1990.*
- Table 4 *Overview of rainfall, ET_o , throughfall, throughfall rain exclusion and throughfall rain reduction expressed in mm of water column or percentage in given period of growing seasons 2011 – 2015.*
- Table 5 *Upper part – relative contribution of 3 biggest trees within particular plot to total stem volume mass and annual stem increment. Lower part – relative contribution of the single biggest tree within particular plot to total stem volume mass and annual stem increment.*
- Table 6 *Stool mortality at particular block and treatment during years 2011-2015.*
- Table 7 *Example of input file for gap filling.*
- Table 8 *Seasonal summary of F_s , ($cm^3 m^2 s^{-1}$) in terms of mean, median and maximal values averaged per treatment.*
- Table 9 *Comparison of daily mean sap flow (Kg), seasonal sap flow totals (Kg) and diameter (mm) at breast height (measured at 130 cm) of particular tree during period July–September in years 2013–2015. Horizontal bars represent relative range of particular value compared to the maximum value within each column. Note the tree S1 (bottom line) which exhibited exceptionally high sap flow rates in all years.*
- Table 10 *Seasonal totals of precipitation, ET_o and transpiration at particular treatment and block.*

Appendix C: List of figures

- Figure 1 *Comparison of two monthly Palmer indices (the PDSI and the Z Index) over period 1961-2014 at Domanínek locality.*
- Figure 2 *Comparison of PDSI and Z Index in months May and June over period 1961–2014 at Domanínek locality with marked trend lines.*
- Figure 3 *Monthly course of average air temperature and precipitation totals compared to climatological normal 1961–1990.*
- Figure 4 *(A) experimental design layout. (B) aerial footage of 1 ha experimental plantation with marked positions of experimental Blocks (replications). Arrows indicate sloping terrain, along which water leaves the area. (C) Block 1 with 40 % throughfall exclusion in 2011. (D) Block 1 with 70 % throughfall exclusion in 2015.*
- Figure 5 *Airborne image of soil moisture monitoring access tubes locations.*
- Figure 6 *Final allometric relationship based on datasets from 2011, 2013 and 2016.*
- Figure 7 *Boxplot showing seasonal (2012-2015) soil moisture of control and throughfall exclusion treatments of Block 1-3 in layer 0-45 cm.*
- Figure 8 *Seasonal course of soil water potential (SWP) profile at throughfall exclusion treatment (R) in depths 0.1, 0.2, 0.3 and 0.4 m. In 2011 and 2012 only 40 % of the plot was covered, since June 2013 70 % was covered which resulted in earlier and more severe incidence of water shortage in seasons 2014 and 2015 at R plot. Note, that SWP is in fact negative, therefore, numbers on y axis represent negative values of SWP.*
- Figure 9 *Initial (June 2011) and final (Oct 2015) standing stock of control and throughfall exclusion treatment, expressed in tons of dry matter per hectare.*
- Figure 10 *Annual above-ground biomass productivity of control and throughfall exclusion treatments of individual blocks.*
- Figure 11 *Comparison of tree diameter distribution of control and throughfall exclusion treatments within particular blocks in the beginning (2011) and the end (2015) of the experiment.*
- Figure 12 *Cumulative distribution of stem mass is linked to the cumulative distribution of stem growth. Each blue and red dot represents a single tree (stem) growing within C and R treatment of respective Block. Box in the right-down corner of each graph contains Gini coefficients (Katholnig, 2012), quantifying the heterogeneity of trees within particular plot.*
- Figure 13 *Stool mortality of control and throughfall exclusion treatment during at the end of growing seasons 2011–2015.*
- Figure 14 *Typical configurations of simulated temperature field (tangential cross-section 1.5 cm from stem surface) for needle (a), (b), plate (c), (d) and volume (e), (f) heating for sap flow 0 (a), (c), (e) and 30 (b), (d), (f) g cm⁻² h⁻¹. Bold segments (c), (d) and rectangles (e), (f) present heated domain (Tatarinov et al., 2005).*
- Figure 15 *The temperature difference (ΔT) between the heated and unheated probe as a function of sap velocity (Clearwater et al., 1999).*
- Figure 16 *Configuration of Granier-type system for sap flow measurement (Lu et al., 2004)*
- Figure 17 *Gap filling software – user interface.*

- Figure 18 *An example of daily course of temperature difference (ΔT) of 2 randomly selected sensors (solid lines) in summer 2013. Dashed lines represents daily maximum temperature difference (ΔT_{max}), which are used for calculation of sap flux density (F_d).*
- Figure 19 *An example of daily course of sap flux density (F_d) of 2 sensors, calculated according to ΔT and ΔT_{max} , from previous Figure.*
- Figure 20 *Average sap flux density (F_d) of an average day over 15 day period, as measured by 4 sensors installed at different orientation of a tree circumference and different sapwood depth. The black solid line represents sensor installed from northern side of a tree, measuring in the outer sapwood ring (0–20 mm). The black interrupted line represents sensor installed from southern side, measuring in the outer sapwood as well. The grey solid line stands for sensor installed from northern side, measuring in the inner sapwood ring (20–40 mm). The grey dashed line is sensor installed from southern side, measuring in the inner sapwood as well. Parameter a = ratio of average inner versus average outer F_d , parameter b = ratio of average outer F_d measured from northern and southern direction, parameter c = ratio of average inner F_d measured from northern and southern direction.*
- Figure 21 *Daily transpiration (mm) of control and throughfall exclusion treatment in Blocks 1, 2 and 3, during growing season 2012.*
- Figure 22 *Daily transpiration (mm) of control and throughfall exclusion treatment in Blocks 1, 2 and 3, during growing season 2013.*
- Figure 23 *Diurnal courses of ET_o , transpiration of control (C) and throughfall exclusion treatment (R) shows 30 days without rain following after an abundant rainfall (47.5 mm on June 28th 2013). Note, that shortly after rain the ET_o , C and R have similar magnitude. As the time proceeds, transpiration of C and especially R (receiving 70 % less throughfall precipitation) water declines.*
- Figure 24 *Daily transpiration (mm/m²/day) of control and throughfall exclusion treatment in blocks 1, 2 and 3, during growing season 2014.*
- Figure 25 *Daily transpiration (mm/m²/day) of control and throughfall exclusion treatment in Blocks 1, 2 and 3, during growing season 2015.*
- Figure 26 *Comparison of daily transpiration rates of control and throughfall exclusion treatment during growing seasons 2012–2015.*
- Figure 27 *Daily transpiration (mm) of control and throughfall exclusion treatment on monthly basis during growing seasons 2013–2015.*
- Figure 28 *Comparison of daily transpiration rates of control and throughfall exclusion treatments in particular Blocks. Data include growing seasons 2012–2015.*
- Figure 29 *Relationships between water-use efficiency and average seasonal soil moisture at particular C and R treatment of block 1 and block 3. There can be seen how decreasing soil moisture enhances water-use efficiency.*

ANNOTATION

This thesis comments on agrometeorological factors influencing growth and development of poplar-based short rotation coppice, grown in Bohemian-Moravian highlands in the Czech Republic. The principal argument for growing of this low demanding agricultural crop is production of woody biomass on marginal agricultural land. The widely accepted concern is that the main limit of biomass productivity is water availability. Thus, the general objective of this thesis was to study responses of poplar short rotation coppice (SRC) to adverse conditions, which might be brought by future climate, in a way of simulating of such conditions *in situ*. Therefore a three-times replicated throughfall-rain exclusion experiment with split-block design, comprising a control treatment with intact rainwater income (C) and reduced throughfall rainwater income (R) was established in 2011. During the experimental phase (2011–2015) a tree- and stand-water use was monitored using sap flow heat dissipation method and annual productivity of harvestable biomass was measured as well. Both combined provided information about water-use efficiency (WUE). The above-ground biomass productivity after 7 years of planting reached 11.70 t ha⁻¹ of dry matter (DMC) for control treatment and 10.72 t ha⁻¹ for droughted treatment, which represents reduction of 8.36 %. Mean seasonal daily water use reached 2.19 and 1.98 mm d⁻¹ for C and R, respectively. The R treatment managed to induce drought stress at 2 experimental blocks, whereas at the 3rd block the soil moisture at R was higher compared to C. During the study period a high variability in productivity of particular experimental plot was observed. Trees showed high level of heterogeneity with strong competitive relationships among neighboring trees, what resulted in formation of several dominant trees. This development was more apparent at R treatment, followed by higher mortality. The mean WUE reached 3.17 and 3.00 g kg⁻¹ for C and R, respectively. However, poplars showed ability to increase WUE up to 5.05 g kg⁻¹ when exposed to severe soil water deficiency. This suggest, that poplar SRC plantations based on hybrid poplar clone *P. nigra* × *P. Maximowiczii* are able to withstand prolonged periods of severe drought stress and still maintain certain level of productivity.